PHILOPATRY AND POPULATION GENETICS ACROSS SEABIRD TAXA

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ABSTRACT

Successful conservation depends on an understanding of dispersal patterns for spatially complex species. Among seabirds there are opposing pressures to either disperse or return to natal colonies. We explored philopatry across 36 species, based on banding and census data. Philopatry correlated with foraging strategy, taxonomy, and region, suggesting that translocation will be more successful for Procellariiformes, those in tropical regions and with non-central foraging strategies, as they are more likely to return to translocation sites. Additionally, we compared genetic diversity between two orders of seabirds with differing philopatry and explored population genetics of a species in the order Procellariiformes, the Band-rumped Storm Petrel (BSTP; *Oceanodroma castro*). Findings indicated no difference in genetic diversity between orders and high genetic diversity within BSTP. Although this study suggests that BSTP are not at risk genetically, they remain vulnerable to threats. Management efforts to ensure successful nesting is crucial to recover the endangered BSTP.

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INTRODUCTION

Knowledge on the dispersal and connectivity of species is a key part of conservation biology and biogeography. Seabirds, spatially complex taxa, are crippled with one of the highest ongoing rates of extinction, and many taxa are under federal protection (Spatz et al., 2014). Nevertheless, seabirds continue to be threatened by commercial fisheries, introduced predators, habitat loss, light pollution, marine debris, and climate change (Croxall et al., 2012). This thesis examines behavioral philopatry and genetic diversity within seabird populations, and how this information can be used to inform best management practices for seabird conservation.

Within long-lived colonial seabird species, there are opposing pressures to either disperse to new colonies or return to natal colonies. The behavior of returning to the natal breeding site, natal philopatry, usually guarantees resources and mates but also increases the potential for inbreeding, competition, and ecological traps. There are two types of philopatry, genetic and behavioral. Philopatry, as measured by genetic means, is defined as less than one migrant per generation; anything beyond this indicates dispersal (Spieth, 1974; Lewontin, 1974). Behavioral philopatry is measured by the number of individuals that return to their natal site to breed (Weatherhead & Forbes, 1994).

Chapter 1 documents dispersal patterns across 36 different seabird species, based on long-term banding, along with census data. The goal of this chapter is to identify underlying mechanisms driving behavioral philopatry with seabirds. Chapter 2 examines the effects of genetic philopatry between taxonomic seabird orders and within a federally endangered species, the Band-rumped Storm Petrel (BSTP; *Oceanodroma castro*). This is the first study to look at the population genetics of the BSTP across the Hawaiian Islands. The evaluation of genetic structure

in the present *O. castro* colonies in the Hawaiian Islands can help prioritize management efforts toward strategies that will be successful in increasing population size and conserving the current genetic diversity.

CHAPTER 1

DISPERSAL UNDER THE SEABIRD PARADOX: PROBABILITY, FORAGING STRATEGY, OR SPATIAL ATTRIBUTES?

ABSTRACT

An understanding of natal dispersal in spatially structured populations is necessary for successful conservation. Within long-lived colonial seabird species, there are competing pressures to either disperse to novel colonies or return to natal colonies. The behavior of returning to the natal breeding sire, philopatry, usually guarantees resources and mates but also increases the potential for inbreeding, competition, and ecological traps. Thus, the high degree of philopatry among seabird species, coined the seabird paradox, is surprising, given their dispersal capabilities. We evaluated whether seabirds returned to their natal colony at rates greater than those predicted by potential dispersal variables including colony demographics, life history, or geography. We compiled long-term banding and census data from 36 seabird species across 465 colonies. A linear mixed-effects model was employed to determine how dispersal related to colony demographics wing load, foraging strategy, and spatial variables. Our results suggest that philopatric rates significantly differ from those expected based on colony size and demographics, and instead predicted by region, taxonomic order, and foraging strategy. The success of seabird translocation efforts depends on philopatric rates, as seabirds must return to the colony to benefit from predator control and habitat restoration. Our study suggests that conservation translocation programs will be more successful for species in the order Procellariformes, as well as for species in tropical regions, and those with non-central foraging strategies, as these seabird species will be more likely to return to translocation sites.

INTRODUCTION

Seabirds exhibit high rates of colonial philopatry despite high dispersive potential, a phenomenon coined "the seabird paradox" (Milot et al., 2008). Within long-lived colonial species, there are competing pressures to either disperse to a novel colony to breed or return to the natal colony. Individual colonies are not always discrete populations and dispersal to other colonies is usually made by young seabirds before breeding for the first time (Schreiber & Burger, 2002). Advantages of dispersal, recruitment to breed at a new site, include the potential to minimize inbreeding and competition, but dispersal also comes with a high risk of mortality. Philopatric behavior, where individuals return and recruit to their natal breeding ground, usually guarantees resources and mates but also increases the potential for inbreeding, competition, and ecological traps under climate and land use change. Thus, the high degree of philopatry among seabird species is surprising, given their dispersal capabilities (Milot et al., 2008; Weimerskirch et al., 1984; Fisher, 1976; Huyvaert & Anderson, 2004; Frederiksen & Peterson, 1999).

A recent review (Coulson, 2016), suggests that previous estimates of philopatry may be inflated within seabird species due to the failure to consider factors that may influence coloniality. Colonial breeding, a complex behavior exhibited by the majority of seabirds, is based on an evaluation of site-based factors. The "commodity selection" theory (Danchin & Wagner 1997) suggests that colonial animals assess environmental conditions to choose where to breed, considering environmental conditions such as nesting habitat, shelter, predator avoidance, food, and mates. Likewise, colonial nesting areas such as steep cliffs or isolated islands may be selected due to a lack of predators. Hence, when assessing philopatric rates to seabird colonies, one should consider the quality and condition of the natal colony.

Variation in philopatric rates across taxa may also be due to other dispersal-associated variables (Coulson, 2016). For example, wing morphology, linked to the ability to fly, may influence bird migration (Berthold, 1996). By comparing body mass over wing surface area, or wing load, to dispersal distance among species, we can determine what portion of dispersal within a species is explained by wing load. Additionally, foraging mode, central foraging within near shore waters versus non-central foraging in pelagic offshore waters, may influence dispersal. Central-place foragers (i.e. Sterna, Pelecaniformes, Sula, etc.) may have lower rates of philopatry because they must follow the food immediately around their nesting sites (Jovani et al., 2016; Elliot et al., 2009; Wakefield et al., 2017). Seabirds that are dietary generalists, switching from terrestrial to at-sea foraging, feed in areas adjacent to the colony (Isaksson et al., 2016). In contrast, other seabirds, including Procellarid species, forage hundreds, or even thousands of kilometers away from their colonies and are thus less dependent upon local food shifts (Freeman et al., 2010; Young et al., 2009; Froy et al., 2015).

Region, associated with particular environmental conditions, may be correlated with philopatry due to environmentally-influenced factors. For example, tropical waters generally have a lower productivity and more patchy distribution of resources than polar or temperate regions (Weimerskirch, 2007), leading to differences in foraging and breeding behaviors. Lower resource availability in the tropics lengthens breeding cycles (Reynolds et al., 2014; Nisbet & Ratcliffe, 2008) and many tropical species also exhibit asynchronous breeding cycles which are thought to be tied to resource availability. Tropical seabirds forage greater distances than temperate seabirds, due to lower resource availability (Nelson, 1983). For example, Procellariiformes that breed in the tropics feed in productive high latitude regions during the nonbreeding season (Conners et al., 2015). Seabirds breeding in the tropics may even shift

foraging activities outside of the breeding season, due to low resource availability, or may shift their breeding season entirely to track resources (Nelson, 2005). In contrast, temperate seabirds are synchronous due to the short availability of food for their offspring in the temperate summer. Temperate seabirds tend to breed within or close to colder, more productive waters and forage less widely than tropical seabirds (Nelson, 1983).

Inter-colony dispersal rates are likely to be affected by factors of colony demographics such as colony size, number of colonies, and space between breeding colonies (Lebreton et al., 1992). We expect a higher probability of dispersal from small to large colonies than from large to small based on the theory of habitat selection shaped by fitness maximization and thus provides access to more mates (Serrano et al., 2005). In support of this, single species social attraction studies and mark-recapture modeling have shown that colony size is a driver in post-fledging dispersal (Fernández-Chacón et al., 2013; Podolsky & Hess, 1992).

In this study, we determined whether seabirds return to their natal colony at rates greater than expected based on demographic colony structure and dispersal factors, including distance, number of colonies, size of each colony, wing load, foraging strategy, taxonomy by order, and region (temperate, tropical). If rates of observed philopatry within seabirds were proportional to colony demographics, we expected a linear relationship of philopatry to relative colony size. If philopatry was consistent with the seabird paradox, we expected consistently high philopatric rates regardless of relative colony size. In contrast, if natal dispersal were random, we expected philopatry to average 50 % in respect to relative colony size (Figure 1.1).

METHODS

Seabird banding and census data

Species were selected based on the availability of data from both long-term census and banding studies. Data were obtained from comprehensive nesting databases as well as long-term banding databases. Nesting databases indicating colony size and location included Hawaiian seabird census data from the Bishop Museum Hawai‘i Biological Survey (Pyle & Pyle, 2017) and British Isles seabird census data from the Seabird 2000 colony census (Mitchell et al., 2004). Banding databases of the associated seabird species were provided by the Bird Banding Laboratory (BBL) for tropical species within the Hawaiian region and by the British Trust for Ornithology (BTO) for temperate species in the British Isles. Banding data from BBL was retrieved May 25th, 2017 (USGS Bird Banding Laboratory, 2017) and banding data from BTO was retrieved July 25th, 2017. Banding recapture data spanned over a century representing a total of 36 seabird species from the orders Phaethontiformes, Procellariiformes, Suliformes, and Charadriiformes, including 19 tropical species and 17 temperate species (Table 1.1) within the British Isles and the Hawaiian Islands (Figure 1.2).

The BBL and BTO banding data were filtered to include all recapture data from individual birds that were banded as fledglings, including dead or alive recaptures. We assumed that if an adult individual was observed at the natal site during the nesting season, it had returned to breed. For BBL data, at-sea captures and those found outside of the Hawaiian colonies were excluded from the final dataset. BTO data excluded at sea captures. Natal philopatry for each species was determined by dividing the number of recaptures at the natal site by the total number of recaptures for the species. For this study, individuals returning to sites under 20 km from their

natal banding location were considered to have returned to the natal site, similar to previous studies (Coulson, 2016). Seabird colonies with less than five recaptures for a given species were removed from the final analysis due to small sample sizes.

Spatial data

For this study, the term "colony" varied by study system due to differences in data collection of colony size. For the tropical seabird dataset, each island was treated as a single colony. For the temperate seabird dataset, each county was defined as a single colony. Distances between colonies were found by calculating the Euclidean distance between center GPS points of the focal colonies (i.e. island or county). Although there was high variability in size of the colonies in both tropical and temperate datasets, there were no outliers within the colony dataset.

Species characteristics: wing load and foraging strategy data

Wing load and foraging strategy for each species were collected from online databases: Cornell Lab of Ornithology – Birds of North America, The Cornell Lab - All About Birds, USFWS Hawaiian Island National Wildlife Refuge – Seabirds, and Wildscreen Arkive – Species (Poole, 2005; The Cornell Lab, 2017; U.S. Fish & Wildlife Service, 2017; Arkive, 2017). Non-central foraging strategy was determined based on taxonomy and published studies using GPS trackers indicating a foraging range over 200 km without consistent trips back to the colony during non-breeding seasons (Adams et al., 2016; Shoji et al., 2016). All Charadriiformes and Phaethontiformes were classified as central foragers while all Procellariiformes were classified as non-central foragers (Guilford, et al., 2008; McDuie et al., 2015; Le Corre et al., 2012). Most Suliformes were central foragers, with the exception of the Northern Gannet (*Morus bassanus*)

and Great Frigatebird (*Fregata minor*); Thaxter et al., 2012; Gilmour et al., 2012). Wing load was calculated as average mass (g) over average wingspan (cm) since wing surface area was not available for most species.

Genetic data

A cladogram for all 36 species of seabirds in this study was built using concatenated nucleotide sequences of mitochondrial genes cytochrome b (cyt *b*), 12S ribosomal RNA (12S), cyclooxygenase (COX), ATP synthase subunit 6 (ATP6), and NADH dehydrogenase subunit 2 (ND2), and nuclear gene recombination activating gene 1 (RAG1). Sequence data from 35 species were obtained from a previously published seabird study (Hughes & Page, 2007). Concatenated nucleotide sequences of the Hawaiian Petrel (*Pterodroma sandwichensis*) were also added to the initially published alignment (NCBI accession numbers: HQ420351-HQ42080, HQ918211-HQ918230, JF264905-JF26972, and JN015536-JN016231). Individual seabird species were then grouped by taxonomic order and aligned to produce a cladogram (Figure 1.3). The tree was constructed using the software program Geneious (Kearse et al., 2012) with a Tamura-Nei model under neighbor-joining tree build method, creating a consensus bootstrap tree with 1000 replicates and a 50% support threshold.

Statistical analysis

We applied principle components analysis and a linear mixed-effects model to the data, depending on the nature of the test variable, to understand each dispersal variable's relationship to philopatric rates among seabird species. We also computed Pearson's correlation coefficient, to measure the strength of variables to philopatry, and effect sizes (Cohen's *d*) to facilitate

comparison across other studies and datasets. All statistical analyses were conducted in the statistical environment of R version 3.3.3 (R Core Team, 2013).

The relationships of variables to rates of philopatry were measured using a linear mixed-effects model. All quantitative variables were transformed to meet the assumption of normality under linear regression using the skewness test for normality (Shapiro et al., 1968). A linear mixed-effects model was developed for the entire dataset and split by region, tropical and temperate, using R package 'lme4'. The linear mixed-effect models allowed for the analysis of philopatry at multiple colonies across species. We designated each species as an individual group to account for potential bias due to the uneven sampling across seabird colonies. Random effects across colonies were grouped by species while explanatory variables were designated as fixed effects. The linear mixed-effects models allowed for variance-weighted averaging by species when determining significance between philopatry and explanatory variables. Multiple iterations of the model were performed, removing non-significant variables one at a time, to produce the model with the best fit.

RESULTS

We evaluated whether extreme cases of behavioral philopatry in seabirds were simply in line with predictions based on colony demographics, or were indeed a paradox. Based on our study, data from banding and census studies suggested that philopatric rates are higher in the tropical region, the Procellariiformes order, and for non-central foragers. Our results indicated the seabird paradox holds true for some seabird taxonomic groups, but not others.

When compared to the relative proportion of individuals in each colony, seabirds returned to their natal colony at higher rates than expected, with Procellariiformes, non-central foragers, and tropical region having a significant effect on philopatry (Table 1.2). Philopatry had a weak slope toward colony size (Figure 1.4). Under the model with the best fit, the significant independent variables explained 49.2% of the variance (R^2=0.492) within philopatry rates. Philopatry was significantly higher in the Procellariiformes order than in the other seabird taxonomic orders (t_{464}= 2.44, P = 0.0211; Figure 1.5). Additionally, seabird philopatry had a significant relationship with region (t_{464} = 2.766, P = 0.0100) and non-central foraging strategy (t_{464} = -2.40, P = 0.0229) (Figure 1.6). When split by region, the same dispersal factors, as well as colony size, were significantly associated with philopatry in the tropical seabird colonies (Table 1.3). For temperate seabird colonies, the only significant relationship to philopatry was that with distance to the closest colony (Table 1.4).

The principle components analysis showed the variation found within the seabird dataset. We saw clustering by taxonomic order based on colony-level quantitative variables (wing load, philopatric rate, colony size, number of colonies, and distance from the natal colony) (Figure

1.7). The first principle component explained 41.8% of the variation within the dataset with colony size and distance having the highest correlation coefficients.

DISCUSSION

We investigated whether behavioral philopatry in seabirds was based on colony demographics or a product of other mechanisms of dispersal. Although not directly proportional, colony size was positively correlated with philopatry rates. This suggested that relative colony size is an important consideration when making inferences about philopatric rates from single study locations, especially large colonies where people might be more inclined to conduct research. This may lead to the conclusion that high philopatric rates are more common in seabirds than actually true (Coulson, 2016).

Both seabirds under the order of Procellariiformes and those exhibiting a non-central foraging strategy returned to their natal colony at higher rates than other seabirds orders (Charadriiformes, Suliformes, and Phaethontiformes) than those with a central foraging strategy. These variables explained 49.4% of variation within philopatric rates of seabirds, which was noteworthy considering the complex behavior of dispersal. As all Procellariiformes in the study were identified as non-central foragers, the results indicated a linked dispersal pattern to taxonomy and foraging behavior. Furthermore, our study validated previously published trends within the Procellariiformes and non-central foragers. Extensive banding records of Albatross families, in the Procellariiformes order, have exemplified the 'seabird paradox', showing over 99% return rates to some colonies (Weimerskirch et al., 1984; Fisher, 1976). Additionally, seabird restoration programs have had the highest success within the Procellaridae family, with translocated chicks returning at high rates to the new colony (Jones & Kress, 2011).

The same relationship between philopatry, foraging strategy, and taxonomic order was found in tropical seabird colonies but not in the temperate seabird colonies, potentially due to the

low sample size of Procellariiformes within the temperate region (*N*=2). Furthermore, the Northern Fulmer (*Fulmarus glacialis*), one of the two species of Procellariiformes in our study surveyed in the British Isles, had a much lower philopatric rate (43%) than other species of Procellariiformes in the study. The Northern Fulmar underwent a recent expansion in the British Isles, suggesting other factors may have driven dispersal, such as a change in food availability, a genotype favoring range-expansion and colonization, or the gradual warming of the eastern Atlantic during the last century (Lloyd et al., 2010). Overall Procellariiformes had high philopatric tendencies, but there were exceptions within the order.

Within temperate seabird colonies, philopatry was positively correlated with the distance to the closest colony. Most seabirds surveyed in the British Isles were central foragers with smaller home ranges, thus having less potential to disperse to colonies at far distances. Potentially, seabirds were more likely to return to their natal colony due to lack of available surrounding colonies within dispersal range. Additionally, other studies looking at seabird dispersal concluded a significant driver was the distance from the source colony, indicating distance may be an important factor for some species, but not all seabirds (Buxton et al., 2014; Oro et al., 2011; Hénaux et al., 2007).

The higher philopatric rates in the tropical region than in temperate colonies may be slightly biased due to higher sampling of Procellariiformes in the tropical region. However, conditions in this region may favor Procellariiformes and philopatric behavior. The difference in predator composition of Hawai‘i, comprised of isolated oceanic islands, and the British Isles, made up of continentally-adjacent islands, is explained by the theory of island biogeography (MacArthur & Wilson, 2016). Seabird colonies in the Hawaiian Islands, hosting a chain of islands remotely isolated in the Pacific Ocean, formed by undersea volcanos, evolved without

connection to a continent and without mammalian predators (Stearns, 1946). In contrast, the British Isles were connected to Europe during the last glacial period by a plateau called Doggerland, allowing for the dispersal of mammalian predators (Montgomery et al., 2014). Hawaiian colonies may have a greater rate of return because they have historically provided a consistently predator-free or minimum-predation nesting habitat. Tropical waters surrounding Hawai‘i have fewer resources than those at high latitudes, but the benefit of nesting in Hawai‘i’s minimum-predation atolls may outweigh the risk, following the foraging/predation risk trade-off behavior (Verdolin, 2006). The risk of predation has been previously shown to influence population movement in terns and skimmers (Coulson, 2016). Additionally, breeding success has been negatively correlated with the abundance of predators (Oro et al., 2011; Smith et al., 2002; McChesney & Tershy, 1998).

Other environmental drivers may also account for the difference in regional philopatry. Many of the seabirds observed in Great Britain and Ireland were coastal, inland, and roof nesters that breed in many locations within a county, allowing more options for dispersal in this region. Coastal seabird colonies tend to be more stable in occupancy than in inland colonies, most likely due to higher predictability regarding access to food in coastal colonies than inland colonies (Schreiber & Burger, 2002). In England and Wales, seabirds readily moved between inland sites, depending on factors such as disturbance and water levels, which may be responsible for the fluctuation in numbers at many colonies (Gribble, 1979). The British dataset contained a high number of inland colonies, while the Hawai‘i dataset had primarily coastal colonies, which may account for some differences in philopatry.

Primary productivity near foraging grounds may also have driven dispersal patterns. In the tropical regions, adults invest less time in intensive chick guarding than temperate seabirds

due to longer foraging trips (Nelson, 1983). For example, Masked Boobies (*Sula dactylatra)* leave their young to forage for food as soon as they can thermoregulate. In comparison, temperate species like the Northern Gannet (*Morus bassanus*) guard offspring continuously until fledging. Also, tropical pelagic Pelecaniformes return to their chick with food less frequently than inshore temperate seabirds (Nelson, 1983). Due to the need to forage for longer durations in the tropics, there may be more pressure for seabirds to leave their young in predator-free colonies, where needs for parental protection are minimal. Similarly, migrating terrestrial mammals in the temperate regions shift migrate during warmer months to high altitude and latitude grazing grounds to give birth in areas of higher quality habitat and lower predation (Fryxell & Sinclair 1988, Sawyer et al. 2009). Foraging and predation risk trade-off behaviors found in herbivorous cervids may similarly be found within tropical seabird colonies (Geist, 1998). Thus, tropical colonies, for example, predator-free remote atolls, may hold higher quality seabird habitat, leading to increased population stability and higher rates of natal philopatry.

We addressed some potential dispersal variables across seabird species in this study, but other confounding variables were likely at play. For example, the presence of other species of seabirds may have influenced philopatry. Congeneric species may act as a social attraction as observed within Short-tailed Albatross (*Phoebastria albatrus*) (Deguchi et al., 2012). In contrast, other seabird species may serve as competitors reducing philopatry. For examples, Wedge-tailed Shearwaters (*Ardenna pacifica*) outcompete Newell's Shearwater (*Puffinus newelli*) for preferred burrowing space (Raine & Vynne, 2016) and Black-legged Kittiwakes (*Rissa tridactyla*) outcompete Common Guillemots (*Uria aalge*) for space during population booms (Durant et al., 2011). Additionally, sex may influence dispersal as seen in other long-lived species (Chang et al., 2014; Bowen et al., 2005). Studies have shown no sex difference (Milot et

al., 2008; Munilla et al., 2016) as well as male-mediated (Greenwood, 1980; Young, 2010) and female-mediated (Steeves et al., 2005; González-Jaramillo & Rocha-Olivares, 2011) within seabirds suggesting species-level variation. Furthermore, changes in food availability highly influence dispersal. For example, young Long-tailed Jaegers (*Stercorarius longicaudus*) have been known to move to new areas where there was higher food availability (Barraquand et al., 2014).

Seabird populations are decreasing globally with many colonies vulnerable to climate change and land-use change, leading to potential ecological traps under continued philopatric behavior (Mitchell et al., 2004). Although philopatry in seabirds is complex, this study indicated that Procellariiformes, non-central foraging behavior, and tropical region may be responsible some of the underlying mechanisms driving natal site fidelity. Continued research on philopatry across multiple spatial scales within more seabird species is required to support these findings. Seabirds return to their natal colony at higher rates than expected based colony size, making seabirds fit candidates for successful translocation, especially those in threatened colonies. Our study suggests that translocation programs will be more successful for species in the order Procellariformes, as well as for species in tropical regions, and those with non-central foraging strategies, as these species are more likely to return to translocation sites.

Table 1.1. Summary of taxa analyzed (*N*=36), with colony and species associated attributes as well as average philopatric rates for species and range at colonies

Species	Order	Region	Foraging Strategy	Wing Load	Number of Colonies	Observed Percent Philopatric	Range of Philopatry at colonies
Sooty Tern (*Onychoprion fuscatus*)	Charadriiformes	Tropical	Central	2.27	11	0.82+/-	0.69 – .96
Gray-backed Tern (*Onychoprion lunatus*)	Charadriiformes	Tropical	Central	4.66	9	0.91+/-	0.88 – 0.97
Arctic Tern (*Sterna paradisaea*)	Charadriiformes	Tropical	Central	2.81	92	0.72+/-	0 – 1
Little Tern (*Sternula albifrons*)	Charadriiformes	Temperate	Central	2.27	15	0.42+/-	0 – 1
Common Tern (*Sterna hirundo*)	Charadriiformes	Temperate	Central	16.38	21	0.18+/-	0 – 0.88
Sandwich Tern (*Thalasseus sandvicensis*)	Charadriiformes	Temperate	Central	1.61	21	0.20+/-	0 – 1
White Tern (*Gygis alba*)	Charadriiformes	Tropical	Central	1.49	11	0.93+/-	0.79 – .99
Black-Headed Gull (*Chroicocephalus ridibundus*)	Charadriiformes	Temperate	Central	4.34	58	0.75+/-	0 – 1
Common Gull (*Larus canus*)	Charadriiformes	Temperate	Central	6.84	66	0.63+/-	0.33 – 0.76
Herring Gull (*Larus argentatus*)	Charadriiformes	Temperate	Central	5.42	100	0.64+/-	0 – 1
Lesser Black-backed Gull (*Larus fuscus*)	Charadriiformes	Temperate	Central	1	31	0.50+/-	0 – 1
Great Black-backed Gull (*Larus marinus*)	Charadriiformes	Temperate	Central	10.78	65	0.55+/-	0.08 – 0.82
Black-legged Kittiwake (*Rissa tridactyla)*	Charadriiformes	Temperate	Central	1.89	90	0.72+/-	0 – .95
Brown Noddy (Anous stolidus)	Charadriiformes	Tropical	Central	9.29	12	0.88+/-	0.57 – .91
Black Noddy (*Anous minutus*)	Charadriiformes	Tropical	Central	16.33	12	0.77+/-	0 – .91
Razorbill (*Alca torda*)	Charadriiformes	Temperate	Central	10.65	51	0.84+/-	0.14 – 0.96
Atlantic Puffin (*Fratercula arctica*)	Charadriiformes	Tropical	Central	1.5	37	0.92+/-	0.38 - 1
Black-footed Albatross (*Phoebastria nigripes*)	Procellariiformes	Tropical	Non-Central	15.89	10	0.98+/-	0.35 - .99
Laysan Albatross (*Phoebastria immutabilis*)	Procellariiformes	Tropical	Non-Central	4.43	6	0.98+/-	0.05 – .99
Tristram's Storm Petrel (*Oceanodroma tristrami*)	Procellariiformes	Tropical	Non-Central	1.55	6	0.97+/-	0.8 – 1
Wedge-tailed Shearwater (*Ardenna pacificus*)	Procellariiformes	Tropical	Non-Central	3.88	18	0.96+/-	0.83 – 1
Newell's Shearwater (*Puffinus newelli*)	Procellariiformes	Tropical	Non-Central	4.74	4	0.88+/-	0.87 – 0.87
Christmas Shearwater (*Puffinus nativitatis*)	Procellariiformes	Tropical	Non-Central	1.49	18	0.91+/-	0.89 – 1

Bulwer's Petrel (*Bulweria bulwerii*)	Procellariiformes	Tropical	Non-Central	2.18	11	0.95+/-	0.89 – 1
Manx Shearwater (*Puffinus puffinus*)	Procellariiformes	Temperate	Non-Central	2.27	15	0.88+/-	0.64 – 1
Northern Fulmar (*Fulmarus glacialis*)	Procellariiformes	Temperate	Non-Central	10.78	65	0.43+/-	0 – 0.61
Bonin Petrel (*Pterodroma hypoleuca*)	Procellariiformes	Tropical	Non-Central	1.61	18	0.99+/-	0.8 – 1
Hawaiian Petrel (*Pterodroma sandwichensis*)	Procellariiformes	Tropical	Non-Central	6.44	8	0.79+/-	0.82 – .82
European Shag (*Phalacrocorax aristotelis*)	Suliformes	Temperate	Central	19.51	52	0.72+/-	0.09 – .82
Great Cormorant (*Phalacrocorax carbo*)	Suliformes	Temperate	Central	4.41	75	0.25+/-	0 – .83
Brown Booby (*Sula leucogaster*)	Suliformes	Tropical	Central	3.04	6	0.89+/-	0 – 1
Masked Booby (*Sula dactylatra*)	Suliformes	Tropical	Central	11.59	11	0.95+/-	0.67 – 0.98
Red-footed Booby (*Sula sula*)	Suliformes	Tropical	Central	6.41	12	0.83+/-	0.62 – .92
Northern Gannet (*Morus bassanus*)	Suliformes	Temperate	Non-Central	21.72	69	0.15+/-	0 – .70
Great Frigatebird (*Fregata minor*)	Suliformes	Tropical	Non-Central	1.37	11	0.42+/-	0 – .6
Red-tailed Tropicbird (*Phaethon rubricauda*)	Phaethontiformes	Tropical	Central	6.88	17	0.94+/-	0.89 – 1

Table 1.2. Dispersal variables from all seabird taxa (*N*=36) with comparison to rate of philopatry using a linear mixed-effects model

Seabird Species from Temperate and Tropical Colonies

Dispersal variable	$\bar{x} \pm SE$	t-value	*P*	Effect Size	Pearson's r
Number of Colonies	4667 ± 1.394e-05	t_{464}=-0.843	0.4082	*d*=1.737	*r*=-0.311
Colony Size	0.204 ± 6.159e-03	t_{464}=1.715	0.0870	*d*=-0.221	*r*=0.162
Distance to Closest Colony	-0.5342 ± 2.446e-01	t_{464}=1.511	0.1314	*d*=-4.445	*r*=0.325
Wing Load	1.639 ± 4.795e-02	t_{464}=0.372	0.7126	*d*=1.754	*r*=-0.021
Foraging Strategy(1)[a]	1 ± 1.569e-01	t_{464}=-2.402	0.0229*	*d*=1.897	-
Taxonomy(2)[b]	2 ± 2.142e-01	t_{464}=0.712	0.4816	*d*=1.461	-
Taxonomy(3)[b]	3 ± 1.224e-01	t_{464}=-0.528	0.6023	*d*=1.461	-
Taxonomy(4)[b]	4 ± 1.824e-01	t_{464}=2.438	0.0211*	*d*=1.461	-
Region(1)[c]	1 ± 8.809e-02	t_{464}=2.766	0.0100*	*d*=1.926	-

[a]1 = Non-Central Foraging Strategy, 2 = Central Foraging Strategy
[b]Taxonomy: 1= Charadriiformes, 2= Phaethontiformes, 3=Suliformes, 4=Procellariiformes
[c]1 = Tropical, 2 = Temperate
*number of colonies, wing load, distance to closest colony, and colony size percentage were transformed to meet assumptions of normality.

Table 1.3. Dispersal variables from seabird taxa in tropical colonies (*N*=19) with comparison to rate of philopatry using a linear mixed-effects model

Seabird Species for Tropical Colonies					
Dispersal variable	**$\bar{x}$ ± SE**	**t-value**	***P***	**Effect Size**	**Pearson's *r***
Number of Colonies	121 ± 0.0004	t_{102}=-1.540	0.1488	*d*=2.394	*r*=0.016
Colony Size	1.047 ± 0.0108	t_{102}=2.078	0.0405*	*d*=0.170	*r*=0.140
Distance to Closest Colony	-0.474 ± 0.5069	t_{102}=-1.344	0.1823	*d*=-6.467	*r*=-0.056
Wing Load	1.570 ± 0.0614	t_{102}=-2.148	0.0557	*d*=1.244	*r*=-0.118
Foraging Strategy(1)[a]	1 ± 0.1752	t_{102}=-3.288	0.0076*	*d*=1.704	-
Taxonomy(2)[b]	2 ± 0.1965	t_{102}=2.057	0.0636	*d*=2.315	-
Taxonomy(3)[b]	3 ± 0.2111	t_{102}=1.627	0.1368	*d*=2.315	-
Taxonomy(4)[b]	4 ± 0.1421	t_{102}=3.826	0.0026*	*d*=2.315	-

[a]1 = Non-Central Foraging Strategy, 2 = Central Foraging Strategy
[b]Taxonomy: 1= Charadriiformes, 2= Phaethontiformes, 3=Suliformes, 4=Procellariiformes
*number of colonies, wing load, distance to closest colony, and colony size percentage were transformed to meet assumptions of normality

Table 1.4. Dispersal variables from seabird taxa in temperate colonies (*N*=17) with comparison to rate of philopatry using a linear mixed-effects model

Seabird Species from Temperate Colonies					
Dispersal variable	**$\bar{x}$ ± SE**	***t*-value**	***P***	**Effect Size**	**Pearson's *r***
Number of Colonies	5950 ± 0.00002	t_{361}=-1.010	0.3365	*d*=2.526	*r*=-0.0231
Colony Size	-0.036 ± 0.11016	t_{361}=0.865	0.3877	*d*=-0.359	*r*=0.0389
Distance to Closest Colony	-0.551 ± 0.27943	t_{361}=2.161	0.0313*	*d*=-4.998	*r*=0.1269
Wing Load	1.658 ± 0.07219	t_{361}=1.365	0.2011	*d*=1.929	*r*=0.0314
Foraging Strategy(1)[a]	1 ± 0.24711	t_{361}=-1.044	0.3189	*d*=2.396	-
Taxonomy(3)[b]	3 ± 0.28667	t_{361}=-1.458	0.1761	*d*=1.370	-
Taxonomy(4)[b]	4 ± 0.19321	t_{361}=1.037	0.3216	*d*=1.370	-

[a]1 = Non-Central Foraging Strategy, 2 = Central Foraging Strategy
[b]Taxonomy: 1= Charadriiformes, 2= Phaethontiformes, 3=Suliformes, 4=Procellariiformes
*number of colonies, wing load, distance to closest colony, and colony size percentage were transformed to meet assumptions of normality

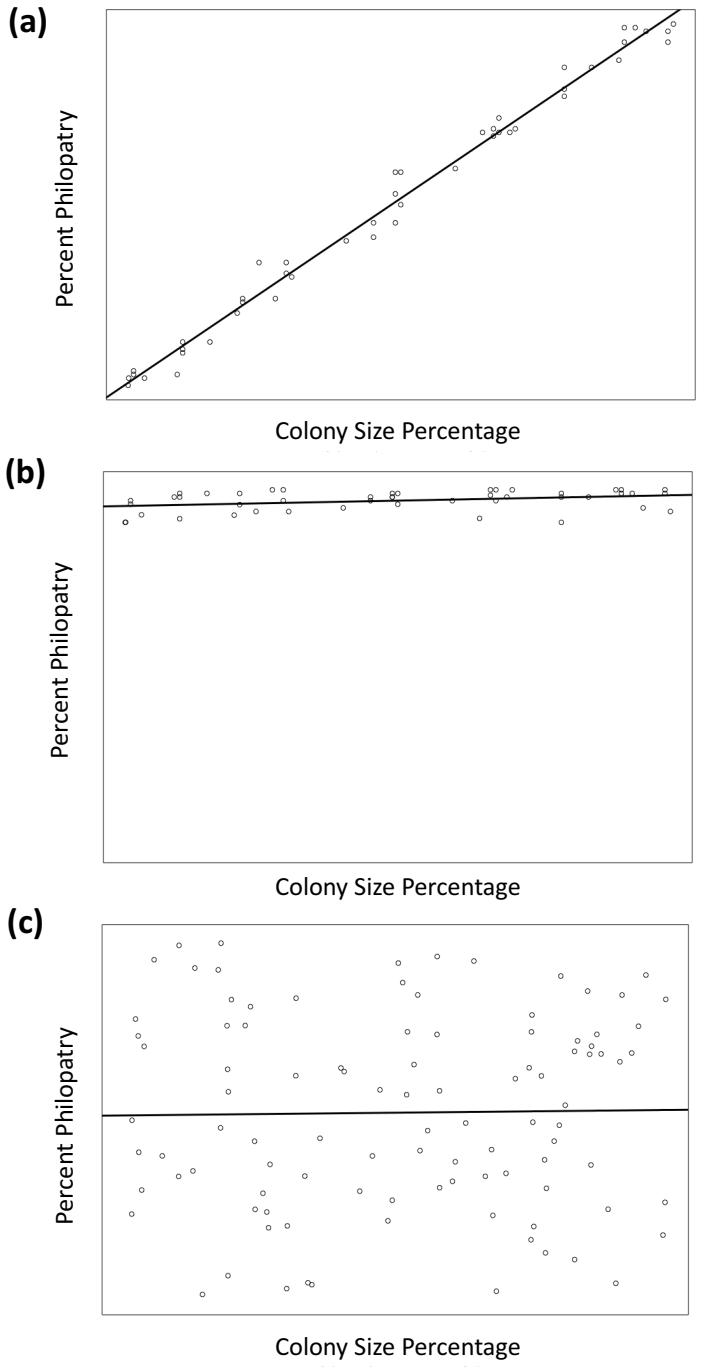

Figure 1.1: Graphs of hypotheses of predicted seabird philopatry as (a) proportional to colony size as percentage, (b) consistent with seabird paradox, and (c) following random distribution

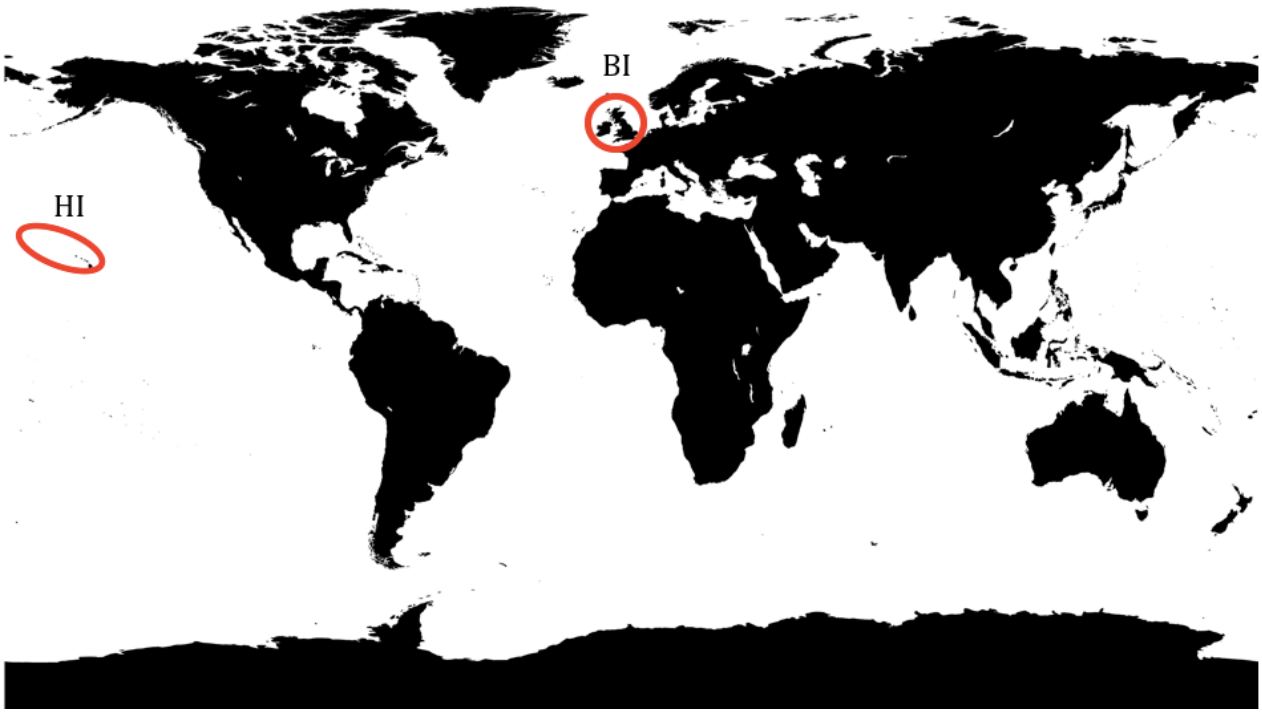

Figure 1.2: Map of locations of all seabird colonies surveyed (*N*=465), with extent indicators on the Hawaiian archipelago (HI) and British Isles (BI)

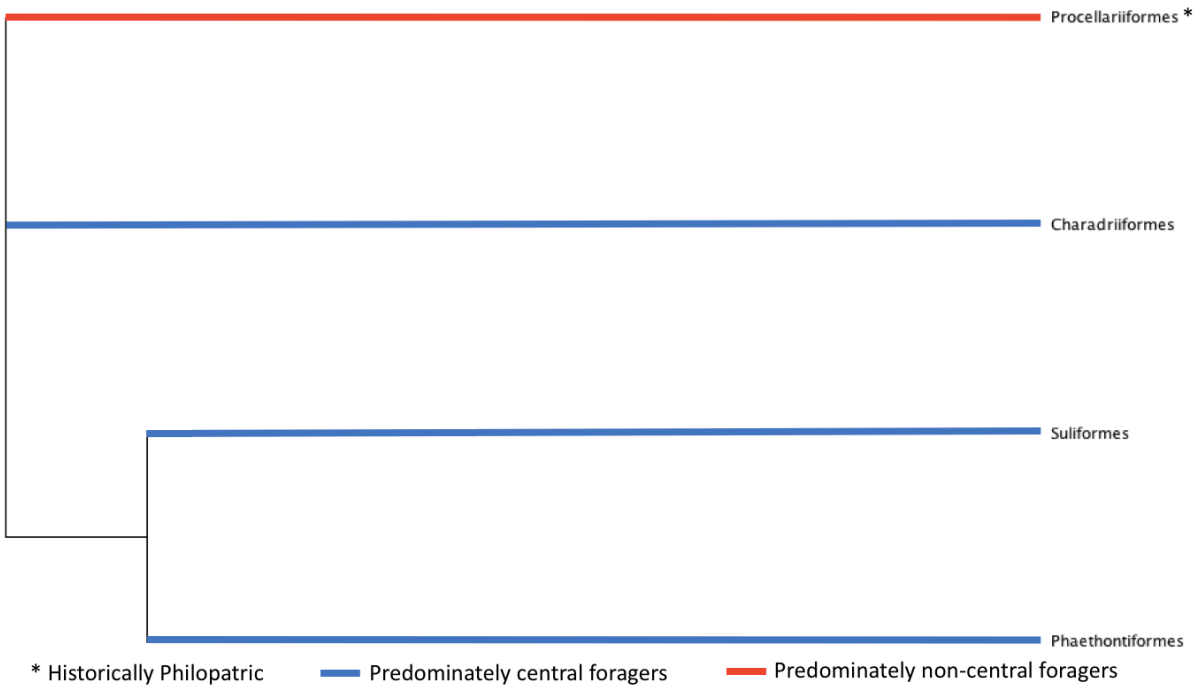

Figure 1.3: Cladogram of all seabird species surveyed (*N*=36) by taxonomic order

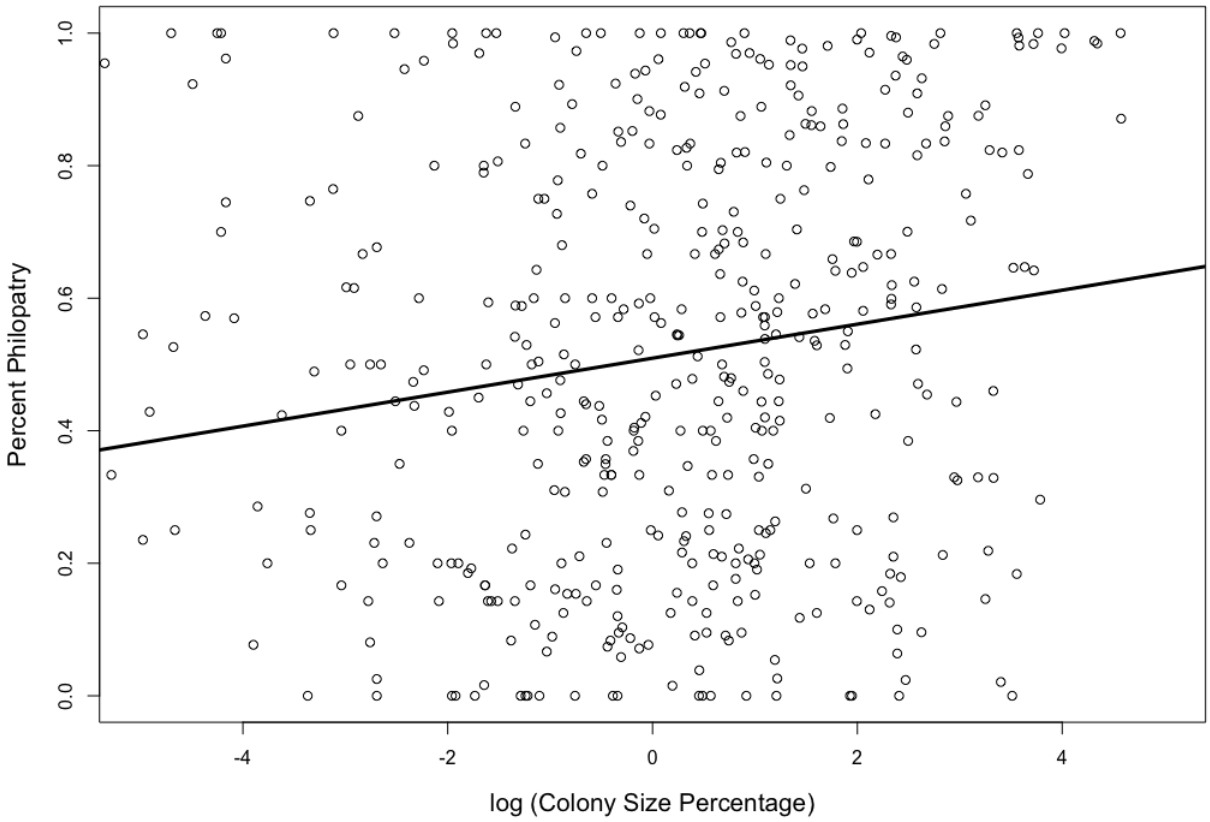

Figure 1.4: Graph of colony size as a percentage of total population size (P=0.0870) compared to percent philopatry to all seabird colonies (N=465). Colony size percentage was log transformed to meet assumptions of normality.

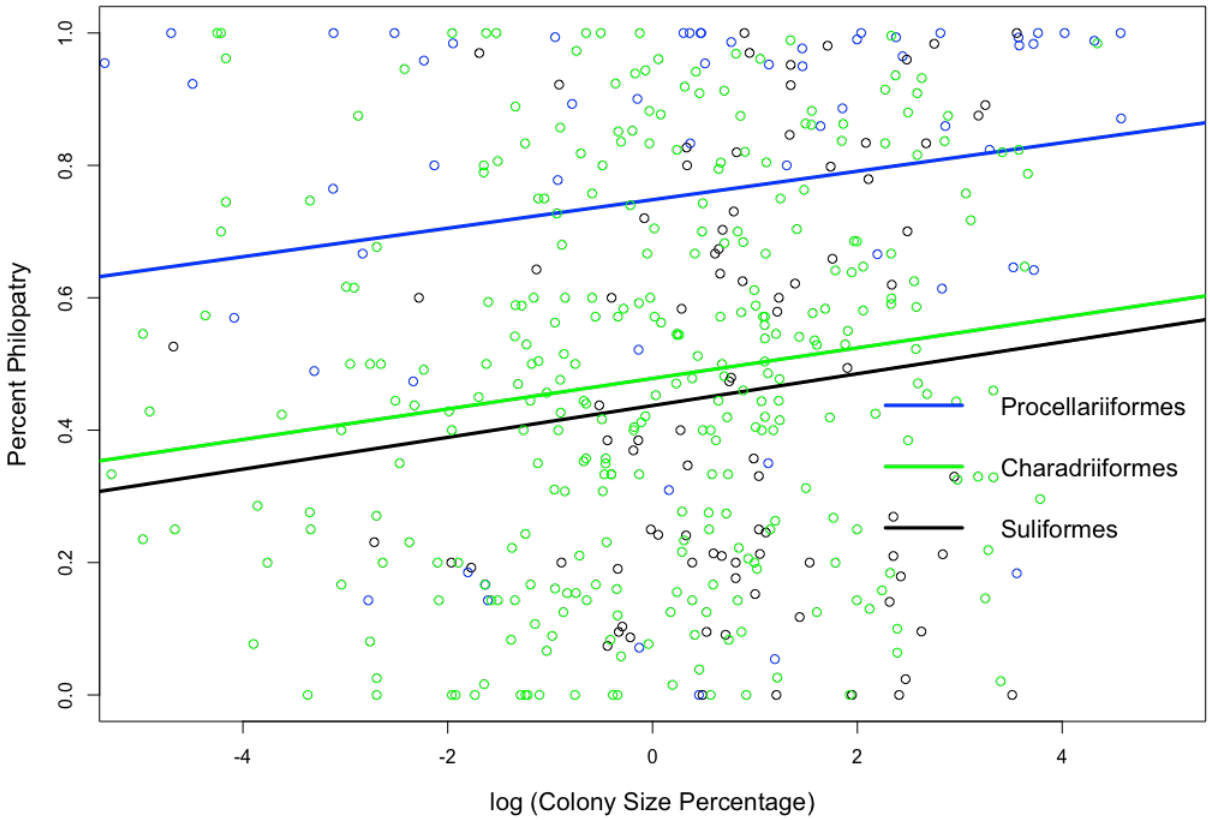

Figure 1.5: Graph of colony size as a percentage of total population size compared to percent philopatry to colonies by taxonomic seabird order. Colony size percentage was log transformed to meet assumptions of normality. Procellariiformes were consistent with the seabird paradox (P=0.0211); However, colony size had a small positive effect on philopatry. The Suliformes and Charadriiformes (P=0.6023) showed no relationship between colony size and philopatry. Phaethontiformes were removed from final analysis because there was only a single species represented.

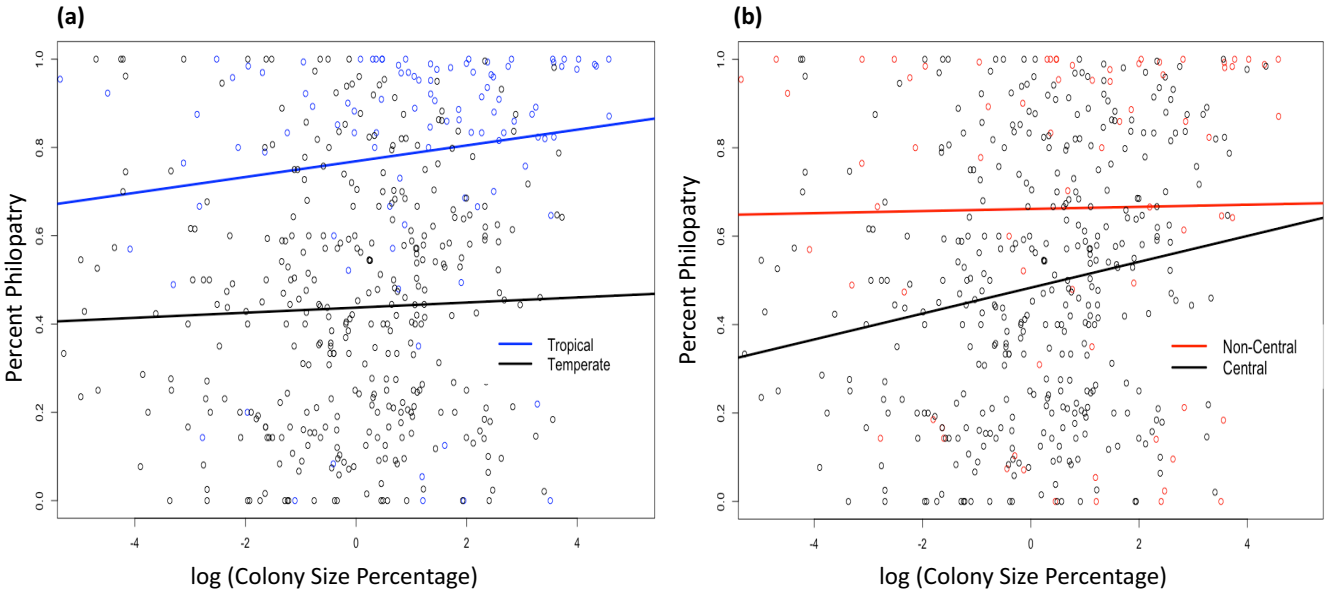

Figure 1.6: Graphs of colony size as a percentage of total population size compared to percent philopatry to seabird colonies by (a) region (P=0.0100) and (b) foraging strategy (P=0.0229). Colony size percentage was log transformed to meet assumptions of normality.

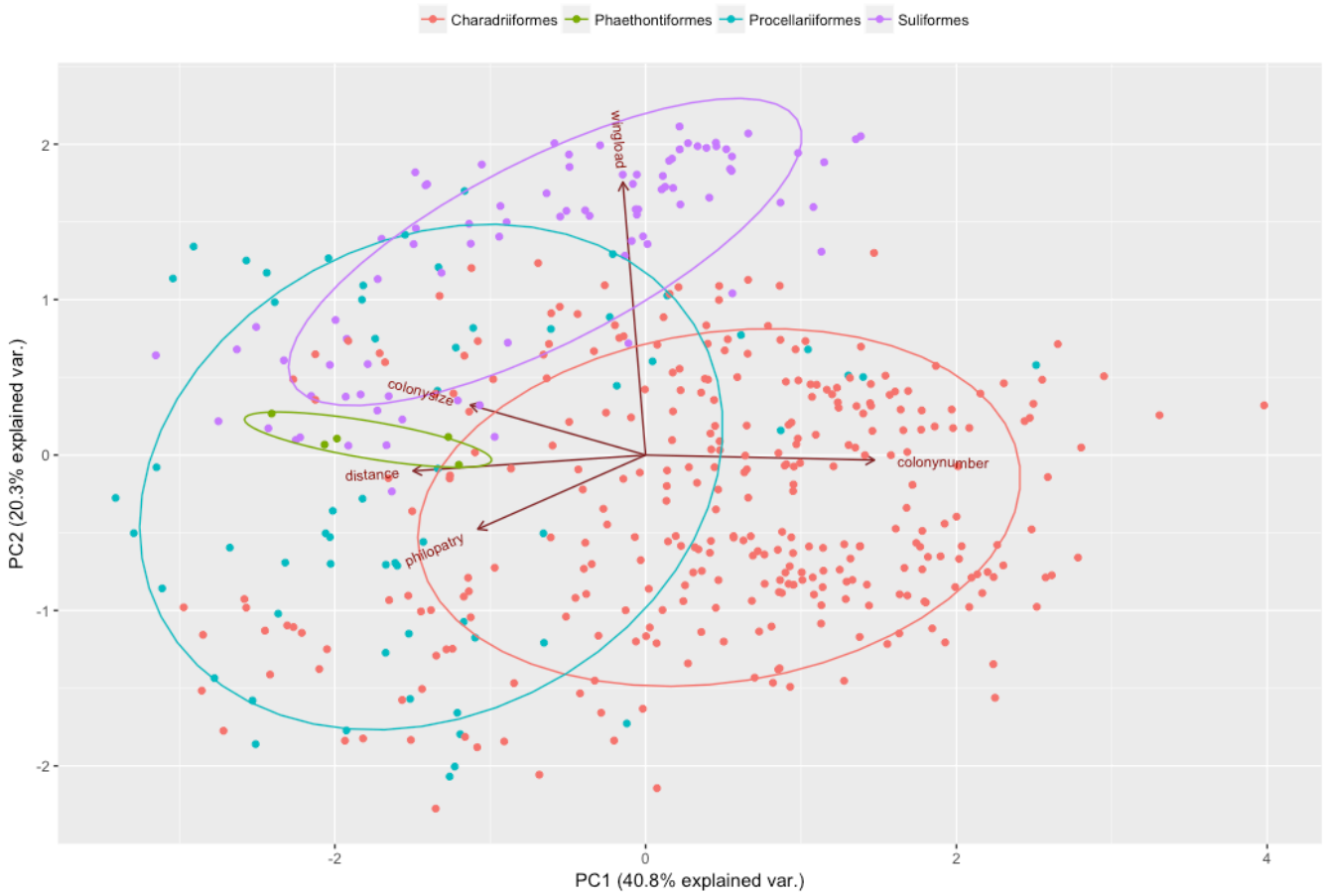

Figure 1.7: Principle component analysis using quantitative variables (wing load, colony size, number of colonies, and distance from the natal colony) from all seabird colonies (*N*=465) grouped by order

CHAPTER 2

POPULATION GENETICS OF THE BAND-RUMPED STORM PETREL (*OCEANODROMA CASTRO*), AN ENDANGERED AND ELUSIVE HAWAIIAN SEABIRD

ABSTRACT

Philopatry, the behavior of returning to the natal site to breed, limits dispersal and presents a conundrum for genetic diversity. A higher degree of philopatry is found within Procellariiformes, a seabird order that comprises of albatross, shearwaters and petrels, storm petrels, and diving petrels. As a high rate of philopatry implies limited dispersal among populations, lower genetic diversity may be expected assuming equilibrium, within Procellariiformes compared to Charadriiformes, a seabird order that includes terns, gulls, and auks that are not considered to be philopatric. Furthermore, species within Procellariiformes that have experienced bottlenecks and thus lowered effective population size would be expected to have even lower genetic diversity. In this study, we evaluated genetic diversity measures in the only known populations of the endangered Band-rumped Storm Petrel (BSTP; *Oceanodroma castro*), a species in the highly philopatric Procellariiformes order. We then compared published genetic diversity measures between species in two orders with divergent rates of philopatry, the Procellariiformes and Charadriiformes, to determine whether genetic diversity is significantly different between these groups. We utilized next-generation sequencing to evaluate patterns in genetic diversity in BSTP populations on the only two confirmed islands to host breeding populations. Results indicated moderate genetic differences between populations and higher genetic diversity than expected. Furthermore, we found no difference in genetic diversity between species in the order Procellariiformes and those in Charadriiformes, contrary to predictions based on significant differences in philopatric rates. Although species may be behaviorally philopatric, the variation within genetic diversity within Procellariiformes indicated that they are not genetically philopatric. This may be explained by sex-biased gene flow or other

mechanisms of complex population structure. Findings from this study may be used to inform seabird conservation efforts, especially those managing genetic diversity and connectivity of threatened colonies.

INTRODUCTION

Philopatry, the behavior of returning to the natal site to breed, may provide predictable resources, mates, and safety, but also increases the potential for inbreeding, competition, and ecological traps if habitat has since been degraded. Highly philopatric species, which limits migration, may thus have lower genetic diversity than related species with higher rates of gene flow (Mitton, 2001). A significantly higher rate of philopatry is found in species in the order Procellariiformes, compared with other seabirds (Chapter 1). Philopatry has been found to influence genetic patterns in some Procellariiformes (Ovenden et al., 1991; Levin & Parker, 2012; Welch, 2011; Milot et al., 2008). As philopatry limits dispersal between populations, lower genetic diversity would be expected within Procellariiformes compared to Charadriiformes (Chapter 1).

Species that have undergone historical bottlenecks, significantly decreasing population size, are more likely to have decreased effective population and have even lower genetic diversity (Avise, 2012). Effective population size is the number of breeding individuals in a population while population size the number of individuals in a population. Given a high rate of philopatry, combined with a historic bottleneck, we would predict that endangered species in the order Procellariiformes would have lower measures of genetic diversity than other species without these risk factors (Mitton, 2001; O'Brien, 1994). The Band-rumped Storm Petrel (BSTP; *Oceanodroma castro*), an endangered seabird in the order Procellariiformes that nests on the Main Hawaiian Islands, is predicted to have low genetic diversity based on its Endangered status, an assumed low population number due to low rates of detection, presumed historical population loss based on previous records and presence in midden sites across the Main Hawaiian Islands

(Pyle & Pyle), and an expected high rate of philopatry similar to closely related species (Friesen, 2015). The endangered BSTP is among the least commonly observed nesting seabirds in Hawai‘i, and therefore difficult to study, with only two confirmed burrows known in the Hawaiian Archipelago (Galase et al., 2017). One of the only tools currently available to assess the remaining individuals is those of genetics. With potentially only a limited number of individuals remaining (Pyle & Pyle, 2017), the populations may have problems normally associated with small numbers, including demographic stochasticity and inbreeding (Kennedy, 2009). In this study, we sampled 10 of the remaining individuals (five per island) to evaluate patterns in genetic diversity and connectivity between the two confirmed island populations in the Hawaiian Archipelago.

The objectives of this study were to: (1) evaluate genetic diversity in an endangered species, the BSTP, with a high rate of philopatry and potentially recent decline (Pyle & Pyle, 2017); (2) develop microsatellite markers useful for population-level studies, to complement nuclear and mitochondrial markers developed for a global study of BSTP (Smith, 2007); (3) compare genetic structure of BSTP populations in the Hawaiian Archipelago to global populations of *O. castro*; and (4) compare genetic diversity between species in the orders Procellariiformes with Charadriiformes, to evaluate predictions based on differing rates of philopatry between these groups.

METHODS

Sample collection

Source populations of BSTP included slot canyons along the Honopu Valley and Waimea Canyon on the island of Kauaʻi and breeding areas on the Pōhakuloa Training Area (PTA) on the island of Hawaiʻi, the only two confirmed breeding populations in the Hawaiian islands (Figure 2.1). Kauaʻi and Hawaiʻi islands represent the northern and southern extent of the main Hawaiian Islands and are approximately 300 miles apart (Figure 2.1).

Blood samples from the metatarsal vein from individuals on Kauaʻi were collected by the Kauaʻi Endangered Seabird Recovery Project, a Hawaiʻi Department of Land and Natural Resources, Division of Forestry and Wildlife project, from birds captured using conspecific playback and mist-netting techniques. Blood samples from one BSTP at Porters Landing Zone (LZ), Waimea Canyon and four individuals from Honopu, Kauaʻi were stored on filter paper. One other sample, supplied by the Kauaʻi Endangered Seabird Recovery Project, was a blood sample collected from a downed fledgling from Kauaʻi. Samples from individuals on Hawaiʻi island were collected by the PTA Natural Resources Office, using dog and personnel searches. Samples included flight feathers from five individuals, collected from individual carcasses or found near nest sites, from the southeast portion of PTA.

Laboratory analyses

DNA was individually extracted from the blood and feather samples using the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) according to the manufacturer's protocol. The extracted DNA was quantified with the AccuClear™ Ultra High Sensitivity dsDNA Quantitation

Kit (Biotium, Hayward, CA) using two rows of eight standards. Due to low DNA yield, whole genome amplification was performed on individual samples with the REPLI-g UltraFast Mini-kit (Qiagen, Valencia, CA) which effectively increases yields of high-fidelity DNA (Ahsanuddin et al., 2017). Equimolar amounts of whole genomic DNA extracted from five blood samples from Kauaʻi and five feather samples from Hawaiʻi island were pooled by their respective population (Kauaʻi, Hawaiʻi) using the ezRAD protocol (Toonen et al., 2013) version 2.0 (Knapp et al., 2016). The two pooled libraries were then digested with the frequent cutter restriction enzyme DpnII from New England Biolabs® (Ipswich, MA) and fragments between 300 and 700 bp in length were prepared for sequencing on the Illumina®MiSeq using the Kapa Biosystems (Wilmington, MA) Hyper Prep kit. Laboratory work was conducted at the Hawaiʻi Institute of Marine Biology (HIMB) in the ToBo Lab at Coconut island in Kāneʻohe Bay, Oʻahu, Hawaiʻi. Libraries were sent to Genetics Core Facility at HIMB and sequenced on the Ilumina®MiSeq platform.

Genetic data analyses

Next-generation sequencing resulted in a total number of 9,266,904 paired-end reads. The *dDocent* pipeline (Puritz, et al., 2014) was applied using the command-line environment in a Unix-based system to assemble loci and detect single nucleotide polymorphisms (SNPs) within the aligned sequences. Trimmed alignments were transformed to be run in Popoolation1 (Institute of Population Genetics, Vienna, Austria) and Popoolation2 (Institute of Population Genetics, Vienna, Austria), using a sliding window analysis for measures of diversity including fixation indices (F_{ST}), nucleotide diversity (π), Watterson estimator of diversity (θ), and Tajima's D (D_T).

The number of SNPs shared between populations ranged from 4,672 at a minimum coverage depth of 4x to 75 at a minimum coverage of 60x and maximum coverage of 200x. For the subsequent analyses, we used a minimum coverage cutoff of 10 reads per nucleotide position, which resulted in a total of 1,431 shared SNPs with 10 – 200x read coverage. We then calculated genetic diversity indices based on 1,970 SNPs within the Hawai'i Island population and 36,572 SNPs within the Kaua'i population, utilizing Popoolation1 with a 10 – 200x read coverage. We calculated fixation indices based on all 1,431 SNPs shared SNPs utilizing Popoolation2.

The discrepancy between the number of SNPs identified in each population, Hawai'i Island (1,970 SNPs) and Kaua'i (36,572 SNPs) may be due to the state of initial sampling material or population demographics. Samples from Hawai'i Island (*N*=5) included slightly degraded feather samples that were found near nests in the colony. Samples from Kaua'i Island (*N*=5) included fresh blood samples collected from live birds. DNA extracted from feathers has been found to be more questionable in quality than DNA extracted from blood samples, which may account for the difference in observed SNPs (McDonald & Griffith, 2012). Another explanation is that Kaua'i's population is expected to have more individuals (Pyle & Pyle, 2017) and thus a higher effective population size which is more likely to have a higher number of SNPs within the population, causing the discrepancy.

Microsatellite identification was carried out using the pal_finder Perl script on the RADseq reads which were filtered for several parameters: include loci with designed primers; exclude loci where the primer sequences occurred more than once in the reads; only include loci with 'perfect' motifs; and rank by motif size (Castoe et al., 2012). Default parameters included optimal 50% GC percent for primers, 18 bp as the minimum length of primer, and an optimal melting temperature of 60 degrees Celsius to identify at minimum six perfect dinucleotide repeat

units. PANDAseq was also utilized to filter out the best quality microsatellite in the reads. PANDAseq identifies 'perfect' microsatellite markers as those with highest-quality bases, checked for sequencing errors, and that contain suitable overlap (Masella et al., 2012). Mircosatellites were not scored in this study but instead identified for the use in future studies.

To compare relationships among global populations with populations in this study, NGS sequences for populations in the Hawaiian Archipelago were aligned to sequences from global populations of *O. castro* accessible in GenBank (accession numbers: KU217330-KU217328, KU863867-KU863946, KU863779-KU863846, KU863964-KU863985) using Geneious 6.0 (Biomatters, Newark, NJ). Construction of phylogenetic trees was carried out with MEGA7 (Kumar et al., 2016) using the Hawaiian Islands population along with those available in GenBank (Azores, Galapagos, and Japan) (Fig. 2.2).

To isolate sequences from mitochondrial regions cytochrome *b* (cyt *b*) and control region (CR) for comparison to other population genetics studies, our next-generation reads were aligned to previously published cytochrome *b* and control region I & II sequences (accession numbers: KU217339 & AY600297) in Geneious 6.0 (Biomatters, Newark, NJ). Overlap included a fragment of cytochrome *b* (177 bp) and a fragment of control region I & II (236 bp). Mitochondrial DNA fragments of cytochrome *b* and control region I & II were concatenated, forming a 416 base pair region that was analyzed for population genetic diversity statistics using TASSEL (Bradbury et al., 2007). TASSEL was implemented as it was designed to analyze isolated genetic sequences, similar to other mitochondrial marker studies.

Other seabird mitochondrial studies

Population diversity statistics were compared between species in the seabird orders Charadriiformes and Procellariiformes. Following a literature search of Web of Science, Google Scholar, and OneSearch Mānoa, 44 published papers were identified that contained genetic diversity measures for species in the seabird orders Charadriiformes and Procellariiformes. Population genetics studies were included if they reported nucleotide diversity (π) population statistics and surveyed a minimum of two populations. Majority of seabird population genetics studies were based on mitochondrial genes. Only studies that included the mitochondrial control region and cytochrome *b* were chosen to limit mutation rate bias. Some studies only supplied a combined average nucleotide diversity for sequences from both the mitochondrial control region and cytochrome *b*. In studies that gave estimates individually, the average diversity estimate was used to keep with consistency.

We employed an independent samples *t*-test in the R computational environment version 3.3.3 (R Core Team, 2013) to compare the means of nucleotide diversity between two seabird orders, Charadriiformes and Procellariiformes.

RESULTS

O. castro *population genetics*

We identified an F_{ST} of 0.108 (P=0.943) between the two extant Hawaiian island populations, based on 1,431 SNPs. Tajima's D (D_T) was negative for both Kaua'i (-0.112 ± 0.015) and Hawai'i Island (-0.103 ± 0.022). A negative Tajima's D (D_T) indicated an excess of rare alleles within a population. Kaua'i island population had a slightly lower nucleotide diversity (π) (0.003 ± .001) and Watterson estimator (0.004 ± .001) than the Hawai'i island population nucleotide diversity (π) (0.004 ± .001) and Watterson estimator (θ) (0.005 ± .001; Table 2.1).

The concatenated mitochondrial fragments of cytochrome *b* and control region I & II (416 bp) aligned with 13 sequences from this study. Based on these sequences, nucleotide diversity (π) was found to be higher in the mitochondrial regions (0.079), than in the regions across the entire genome as sampled in the next-generation sequencing alignments (Table 2.1). The Watterson estimator (θ) was also higher in the mitochondrial regions (0.132) than across the entire genome (Table 2.1). Tajima's D (D_T) was found to be negative in the mitochondrial region (-0.456) (Table 2.1). This strong of a negative Tajima's D (D_T) indicated an excess of rare polymorphisms, that may be generated by population expansion, selection, or most likely high mutation rate in the species (Wares, 2010).

Microsatellite marker identification

Microsatellite discovery through pal_finder resulted in 6,451 microsatellite loci with generated primers. Those loci filtered through PANDASeq resulted in 153 microsatellite markers with identified primers (S1).

Global O. castro *phylogenetic relationships among groups*

The phylogenetic reconstruction of global populations of *O. castro* (Azores, Japan, Galapagos, and Hawai‘i) was constructed with concatenated alignments of two nuclear markers and one mitochondrial marker using a bootstrap Neighbor-joining Tajima-Nei model with 1000 replicates. The method created a genetic distance matrix based on the number of nucleotide substitutions between each group: Azores, Japan, Galapagos, and Hawai‘i. The phylogenetic tree resulted in clustering of Japanese and Galapagos populations with a bootstrap value of 72. Samples from Japanese and Galapagos populations were more genetically similar to each other than to populations from the Hawaiian Archipelago (Figure 2.3). Populations from the Azores did not cluster to any other population with a significant bootstrap value.

Comparison of genetic diversity between seabird orders

We found 44 seabird population genetics studies that published nucleotide diversities statistics within the control region and cytochrome *b*, resulting in a comparison of 23 species of Charadriiformes and 21 species of Procellariiformes in this study (Table 2.2 & 2.3). Due to the skewness of the data, π values were log transformed to produce a normal distribution assessed with a Shapiro-Wilk normality test. Mean nucleotide diversity (π) was not significantly different between Charadriiformes (0.007 ± 0.005) and Procellariiformes (0.010 ± 0.012) ($P = 0.811$, $t_{43} = 0.241$).

DISCUSSION

Despite their Endangered status with a potentially low population size and philopatric tendencies, we found BSTP in the Hawaiian Archipelago had relatively high genetic diversity and structure given the assumed life history. Furthermore, we did not find behavioral philopatry to have a significant effect on genetic diversity, suggesting other mechanisms were driving genetic diversity within seabirds.

We note that caution should be used when interpreting population genetics statistics for only two populations and especially when inferring biology without demographic history, as F_{ST} is best interpreted in a comparative, or relative, context (Marko & Hart, 2011). However, an F_{ST} greater than 0.05 between these two islands, located at the northern and southern reaches of the main Hawaiian Islands, suggested moderate differences among populations (Hartl & Clark, 1997). Previous RADseq analysis on these species globally indicated distinct population genetic groups with having at least an F_{ST} of 0.14 (Taylor, 2017). Nevertheless, an F_{ST} of 0.108 was higher than expected between two Hawaiian islands 300 miles apart compared to an F_{ST} of 0.14 between Japan and Hawai‘i approximately 4,000 miles apart (Taylor, 2017). Under equilibrium Mills and Alendorf (1996) argue it only requires up to 10 migrants to have an F_{ST} of 0, thus an F_{ST} of 0.108 indicated fewer than 10 migrants a generation within BSTP in the Hawaiian Islands. Although results were based on a small sample size (N=10), other studies have shown even with a small sample size (i.e. two individuals), accurate estimates of F_{ST} can be obtained with a large number of SNPs (≈ 1,500) from RADseq data (Nazareno et al., 2017).

Nucleotide diversity estimates within the BSTP Hawaiian island populations were higher than expected based on nucleotide diversity estimates from global populations of BSTP mtDNA,

other Procellariiformes mtDNA, and other seabirds gDNA. Nucleotide diversity of mtDNA for populations of *O. castro* in the Hawaiian Archipelago (π=0.079) was higher than the average for the global species (π=0.013; Smith, 2007), as well as higher than other Procellariiformes (mean π=0.010; this study). Although we note caution when interrupting mtDNA genetic diversity measurements because the low coverage generated from the NGS data overlap. Nucleotide diversities based on gDNA of *O. castro* in the Hawaiian Archipelago were higher than those found in some studies of other seabird species (Tigano et al., 2017; Dierickx et al., 2015) but not all (Clark, 2017). Moderate rates of nucleotide diversity appeared to be present despite their Endangered status and presumed low population size of the BSTP in the Hawaiian Islands.

Other recent studies found lower genetic differentiation metrics based on a NGS SNPs approach (F_{ST} or Φ_{ST} range: 0.009 - 0.33) compared to those calculated based on only mitochondrial sequences (F_{ST} or Φ_{ST} range: 0.44 – 0.91) for the same species, which was consistent with our findings (Taylor, 2017; Clark, 2017; Tigano et al., 2017; Dierickx et al., 2015). Most RADseq studies find lower values due to sampling across the whole genome which includes both areas of high and low polymorphism, while marker approach studies focus on a few chosen isolated sequences, like the mitochondrial genes, which are often more polymorphic (Cariou et al, 2016). Although we found a difference in magnitude between gDNA and mtDNA for *O. castro*, both produced similar trends in genetic diversity (π, D_T, θ) (Table 2.1).

Although there was moderate genetic differentiation in the populations of BSTP in the Hawaiian Archipelago, a higher genetic structure was found between island archipelagos of this species, as evidenced mitochondrial, microsatellite, and ddRAD analysis (Taylor, 2017). Furthermore, the constructed phylogenetic tree placed samples of the Hawaiian Archipelago

separately from other previously sampled global populations (Galapagos and Japan), which supports the finding that populations from the Hawaiian Islands are genetically less similar to those populations of *O. castro* found globally. Our results supported previous findings identifying *O. castro* in the Hawaiian Islands as a distinct genetic group (Taylor, 2017), but we note caution when interrupting the phylogentic tree (Figure 2.3) as it only consisted of three markers with low coverage due to the broadened use of NGS data in comparison to published markers.

Past research has shown genetic structure within seabird species was less a result of philopatric tendencies, but instead linked to foraging range and non-breeding distribution (Friesen et al., 2007). Genetic differentiation between global populations may be driven by ocean currents and at-sea food abundance (Friesen et al., 2007; Taylor, 2017). Foraging strategy has been correlated to population genetic structure within other marine organisms that rely on cold-water upwelling systems (Cassens et al., 2005, Schlosser et al., 2009, Jeyasingham et al., 2013). Ocean patterns influence foraging strategies, and seabirds exhibiting a local foraging strategy may be more likely to return to breed within their natal archipelago. Thus, low genetic differentiation within Procellariiformes within a focal archipelago may be due to complex population structure (Bowen et al., 2005). Spatially complex marine animals, like seabirds, mandate management to survey and conserve different units critical for population structure.

Although species in the order Procellariiformes are more philopatric on average than Charadriiformes (Chapter 1) nucleotide diversity estimates were not significantly different between seabird orders, in contrast to what has been predicted for highly philopatric species (Ovenden et al., 1991; Levin & Parker, 2012; Welch, 2011; Milot et al., 2008). Nucleotide diversity is driven by dispersal rate as well as the combined impact of effective population size,

mutation rates, and history, all of which are expected to vary across avian species and may be driving the variation within the nucleotide diversity estimates (Nabholz et al., 2009). Currently, of these three (dispersal rate, effective population size, mutation rate), mutation rates are debated to be the best predictor of within-species mitochondrial diversity (Nabholz et al., 2009). Although we only included nucleotide diversity estimates from two different genes in the mitochondrial genomes, these regions have different mutation rates (Friesen et al., 2007). Furthermore, in our comparison of seabirds orders we assumed species were at equilibrium, but if demographic impacts persisted, history may be a stronger force driving the observed patterns (Chan et al., 2014).

Although seabird orders had significantly different philopatric trends (Chapter 1), other factors of migration may be greater drivers of genetic diversity. Banding records showed that no single Procellariiformes was completely philopatric, with some dispersal between colonies in all species (Chapter 1). This study's results suggested only a small amount of gene flow is necessary, less than ten migrants per generation, to homogenize genetic structure throughout the metapopulation (Mills and Allendorf, 1996). Another possible explanation is that seabirds may mate while on visiting forays at neighboring colonies, increasing gene flow, as evidenced by female Laysan Albatross (*Phoebastria immutabilis*) in the Main Hawaiian Islands (Young et al, 2010). Within other philopatric species, it is known that they breed offsite, mating with males from other colonies, prior to returning to a natal site to lay eggs (Bowen et al., 2005). Thus, complex population structure for a species must be taken into account to interpret population genetics.

There are many potential reasons for the high genetic diversity observed within populations of *O. castro* in the Hawai‘i Archipelago. A population bottleneck likely occurred

since the arrival of humans to the Hawaiian Islands 1100 years ago, due to habitat destruction and introduced mammalian predators such as rats (*Rattus* sp.), cats (*Felis castus*) and mongoose (*Herpestes javanicus*) (Pyle & Pyle, 2017). In some cases, relatively high genetic diversity in a rare species can indicate that decline in population numbers was recent (Mortiz, 1994). A second possible explanation may be lengthy generation times, coupled with delayed sexual maturity, that can postpone the loss of genetic variation (Kuo & Janzen, 2004). The Band-rumped Storm Petrel is long-lived and has a generation time of 12 years, leading to overlapping generations (Harrison, 1990). In addition, demography can contribute to the retention of genetic diversity (Goossens et al., 2005). Relatively high genetic diversity despite population decline has been observed in other long-lived seabird species (e.g. the Balearic Shearwater *Puffinus mauretanicus*, Genovart et al., 2007; the Magenta Petrel *Pterodroma magenta,* Lawrence et al., 2017; Buller's Albatross *Thalassarche bulleri*, Van Bekkum, 2006). Furthermore, even though the Band-rumped Storm Petrel most likely experienced population decline in Hawai‘i, there may be more individuals than currently estimated (Pyle & Pyle, 2017), as only a few hundred individuals are needed to capture all of the genetic diversity in population (Gaither et al., 2010).

Further research examining these populations of *O. castro* is recommended to understand the connectivity between islands across the Hawaiian Archipelago. Assessment of genetic diversity on other islands and gene flow among islands, as well as in comparison with extinct colonies using historical samples, will facilitate understanding of the historical genetic context and allow for the creation of haplotype networks and effective population size estimates of the endangered populations. Furthermore, fixed SNPs identified between island populations in this study (N=23) may create valuable diagnostic genetic markers to address evolutionary history and

assign unknown or bycatch individuals to a known extant population. Research adding more individuals from multiple years of sampling will add to and support current findings.

Despite their Endangered status and indication of population loss, this study suggests genetics of *O. castro* in the Hawaiian Islands currently do not warrant management concern. Although BSTP do not appear to be in current danger of a genetically induced extinction vortex, they remain vulnerable to other extinction vortexes (Gilpin & Soulé, 1986). Predator control and related management efforts to ensure successful nesting will be crucial to recover endangered populations of the Band-rumped Storm Petrel.

Table 2.1 Population genetic diversities for *O. castro* in Hawaiian island populations. gDNA refers to the RADseq alignments and mtDNA refers to the concatenated mitochondrial sequence of the control region and cytochrome *b*.

Population	DNA Region	Nucleotide diversity ($\boldsymbol{\pi} \pm$ sd)	Watterson estimator ($\boldsymbol{\theta} \pm$ sd)	Tajima's D ($\mathbf{D_T} \pm$ sd)	F_{ST}
Kaua'i Island	gDNA	0.004 ± 0.001	0.003 ± 0.001	-0.112 ± 0.015	0.108 *P*=0.943
Hawai'i Island	gDNA	0.005 ± 0.001	0.004 ± 0.001	-0.103 ± 0.022	
Kaua'i & Hawai'i Island	mtDNA	0.079	0.132	-0.456	-

***** standard deviation of mtDNA was not included because the software used to produce the genetics diversities, TASSEL, does not report them

Table 2.2 Comparison of mean nucleotide diversity within populations (π) from mitochondrial studies of species in the order Procellariiformes (N=21)

Seabird	Family	Marker	π (range)	Paper
Black-footed Albatross (*Phoesbatris nigripes)*	Diomedeidae	Cyt *b* (609bp)	0.0005 (0.00-0.0012)	Walsh & Edwards, 2005
Black-browed Albatross (*Thalassarche melanophrys*)	Diomedeidae	CRI (219bp)	0.02 (0.008-0.042)	Burg & Croxall, 2001
Grey headed-Albatross (*Thalassarche chrysostoma*)	Diomedeidae	CRI (220bp)	0.03 (.0022-0.040)	Burg & Croxall, 2001
Laysan Albatross (*Phoebastria immutabilis*)	Diomedeidae	CRI (189bp)	0.045 (.030-.059)	Young et al., 2010
Northern Fulmar (*Fulmarus glacialis*)	Procellariidae	CRI (299bp)	0.0107 (0.0079-.0139)	Burg et al., 2003
Cory's Shearwater (*Calonectris borealis*)	Procellariidae	CRI, Cyt *b* (1393bp)	0.0132 (0.0023-0.024)	Gómez-Díaz, 2007
Scopoli Shearwater (*Calonectris diomedea*)	Procellariidae	CRI, Cyt *b* (1393bp)	0.0139 (0.0037-0.024)	Gómez-Díaz, 2007
Cape Verde Shearwater (*Calonectris edwardsii*)	Procellariidae	CRI, Cyt *b* (1393bp)	0.010 (0.003-0.016)	Gómez-Díaz, 2007
Sooty Shearwater (*Puffinus griseus*)	Procellariidae	Cyt *b*, CRII (695bp)	≤ 0.004	Friesen et al., 2007
Balearic Shearwater (*Puffinus mauretanicus*)	Procellariidae	Cyt *b*, CR (1180bp)	0.0144 (0.0015 – .0272)	Genovart et al., 2007
Flesh-footed Shearwater (*Ardenna carneipes*)	Procellariidae	Cyt *b* (858 bp)	0.0036 (.0008-0.00471)	Lombal et al., 2017a
Deserta Petrel (*Pterodroma deserta*)	Procellariidae	Cyt *b*, CO1 (1604bp)	0.0005 (.0003-.0007)	Gangloff et al., 2013
Cape Verde Petrel (*Pterodroma feae*)	Procellariidae	Cyt *b*, CO1 (1604bp)	0.0013 (.0011-.0015)	Gangloff et al., 2013

Zino's Petrel (*Pterodroma madeira*)	Procellariidae	Cyt *b*, CO1 (1604bp)	0.0016 (.0009-.0023)	Gangloff et al., 2013
Providence Petrel (*Pterodroma solandri*)	Procellariidae	Cyt *b* (872bp)	0.0093 (0.0069-0.0117)	Lombal et al, 2017b
Magenta Petrel (*Pterodroma magenta*)	Procellariidae	Cyt *b*, CRI & II (1458bp)	0.01387 (0.0013-.0223)	Lawrence et al., 2007
Hawaiian Petrel *(Pterodroma sandwichensis)*	Procellariidae	Cyt *b* (524bp)	0.00397 (0.00382-0.00409)	Welch, 2011
Gould's Petrel (*Pterodroma leucoptera*)	Procellariidae	CRI, Cyt *b* (1327bp)	0.00115 (0.00063-0.0016)	Iglesias-Vasquez et al., 2017
Leach's Storm Petrel (*Oceanodroma leucorhoa*)	Hydrobatidae	CRI, II (357bp)	0.0055 (0.005-0.007)	Bicknell et al., 2012
European Storm Petrel (*Hydrobates pelagicus*)	Hydrobatidae	Cyt *b* (970bp)	0.0005 (0.0-0.0011)	Cagnon et al, 2004
White-faced Storm Petrel (*Pelagodroma marina*)	Hydrobatidae	CRI, II (522 bp)	0.0075 (.004-.011)	Silva, 2015

Table 2.3. Comparison of mean nucleotide diversity within populations (π) from mitochondrial studies of species in the order Charadriiformes (*N*=23)

Seabird	Family	Marker	π (range)	Paper
Ivory Gull (*Pagophila eburnea)*	Laridae	CR (264bp)	0.0016 (.0005-.0027)	Royston & Carr, 2016
Lesser Black-backed Gull (*Larus fuscus)*	Laridae	CRI, Cyt *b* (1573bp)	0.0028 (0.0018-0.0042)	Liebers et al., 2004
European Herring Gull (*Larus argentatus)*	Laridae	CRI (430bp)	0.0110 (0.001-0.018)	Sonsthagen et al., 2012
Common Gull (*Larus canus)*	Laridae	CRI (430bp)	0.0146 (0.01-0.024)	Sonsthagen et al., 2012
Glaucous-winged Gull (*Larus glaucescens)*	Laridae	CRI (430bp)	0.0137 (0.01-0.021)	Sonsthagen et al., 2012
Glaucous Gull (*Larus hyperboreus)*	Laridae	CRI (430bp)	0.0070 (0.004-0.013)	Sonsthagen et al., 2012
Black-legged Kittiwake (*Rissa tridactyla*)	Laridae	CR I, II, III (773bp)	0.0048 (0.003-0.009)	Patirana, 2000
Red-legged kittiwake (*Rissa brevirostris*)	Laridae	CRI (445bp)	0.0150 (.011-.016)	Patirana et al., 2002
Sooty Tern (*Sterna fuscata*)	Laridae	RFLP, CRI, II, III (1399bp)	0.0210 (.018-.026)	Peck & Congdon 2004; Avise et al., 2000
South American Tern (*Sterna hirundinacea*)	Laridae	Cyt *b*, ND2 (790bp)	0.0012 (0.0009-0.0017)	Faria et al., 2010
Least Tern (*Sternula antillarum*)	Laridae	CR (840bp)	0.0050 (0.001-0.007)	Draheim et al., 2010
Common Murre (*Uria aalge*)	Alcidae	Cyt *b* (204bp)	0.0040 (0.0026-0.0053)	Friesen et al., 1996a
Thick-bulled Murre *(Uria lomvia)*	Alcidae	Cyt *b* (253bp)	0.0076 (0.0036-.0156)	Friesen et al., 1996a
Razorbill (*Alca torda*)	Alcidae	CRI (300bp)	0.0130 (0.0093-.0198)	Moum & Arnason, 2001
Black Guillemot (*Cepphus grylle*)	Alcidae	CRII, III (504bp)	0.0030 (0.00-0.0058)	Kidd & Friesen, 1998
Pigeon Guillemot (*Cepphus columba*)	Alcidae	CRII, III (504bp)	0.0087 (0.0047-.0170)	Kidd & Friesen, 1998

Xantus's Murrelet (*Synthliboramphus hypoleucus*)	Alcidae	Cyt *b* (1045bp)	0.0058 (0.002-0.0094)	Friesen et al., 2007
Ancient Murrelet (*Synthliboramphus antiquus*)	Alcidae	CRI, II, III, Cyt *b* (1132bp)	0.0042 (0.004-0.0044)	Pearce et al., 2002
Marbled Murrelet (*Brachyramphus marmoratus*)	Alcidae	Cyt *b*, CRI (1592bp)	0.0070 (0.0028-.0104)	Friesen et al., 1996b; Friesen et al., 2005
Kittlitz's Murrelet (*Brachyramphus brevirostris*)	Alcidae	Cyt *b* (1045bp)	0.0024 (0.0017-0.0030)	Friesen et al., 1996b
Crested Auklet (*Aethia cristatella*)	Alcidae	CR (408bp)	0.0140 (0.012-0.019)	Pshenichnikova et al., 2015
Whiskered Auklet (*Aethia pygmaea*)	Alcidae	CR (670bp)	0.0052 (.002-.007)	Pshenichnikova et. al., 2017
Cassin's Auklet (*Ptychoramphus aleuticus*)	Alcidae	CR (706bp)	0.0061 (.004-.008)	Wallace et al., 2015

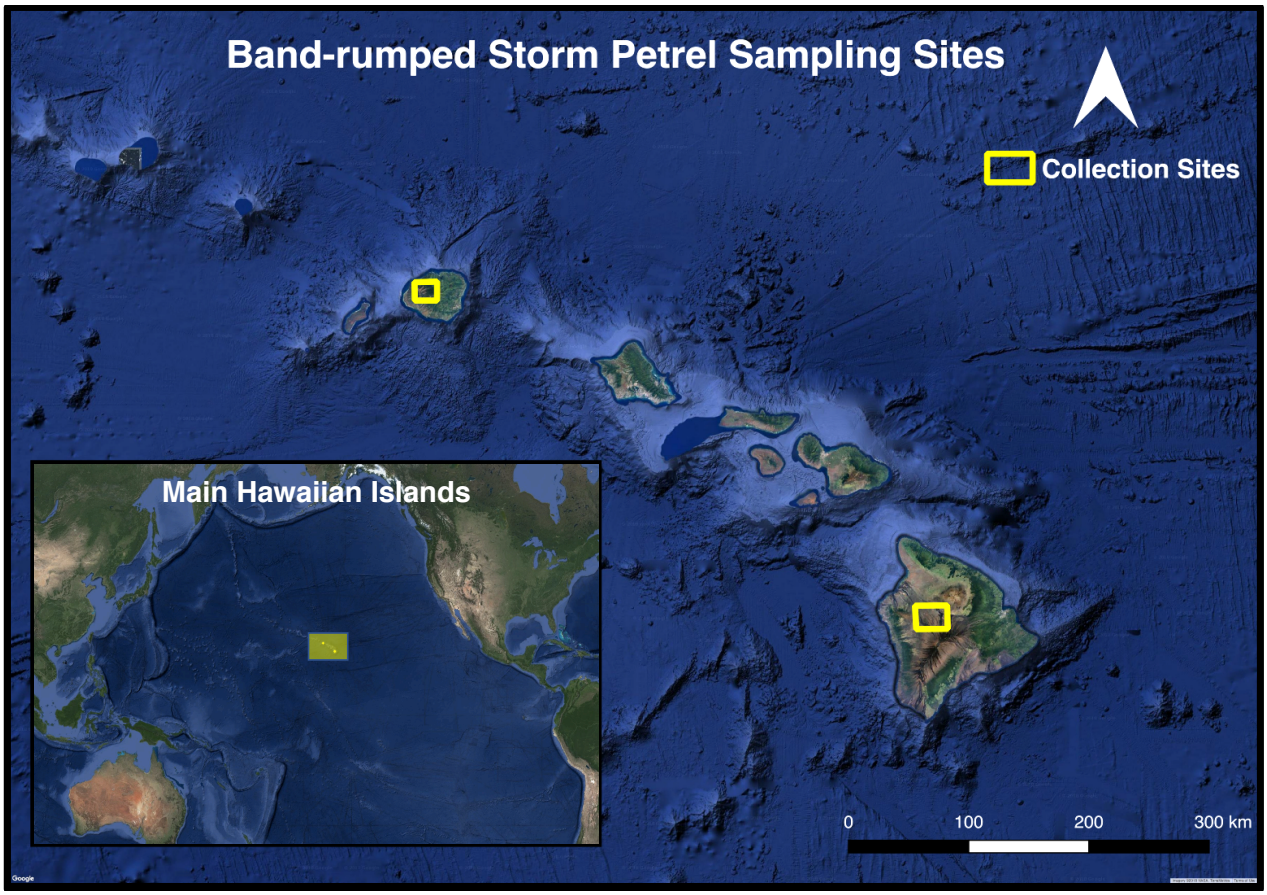

Figure 2.1 Collection sites of the Band-rumped Storm Petrel (*Oceanodroma castro*) across the Main Hawaiian Islands

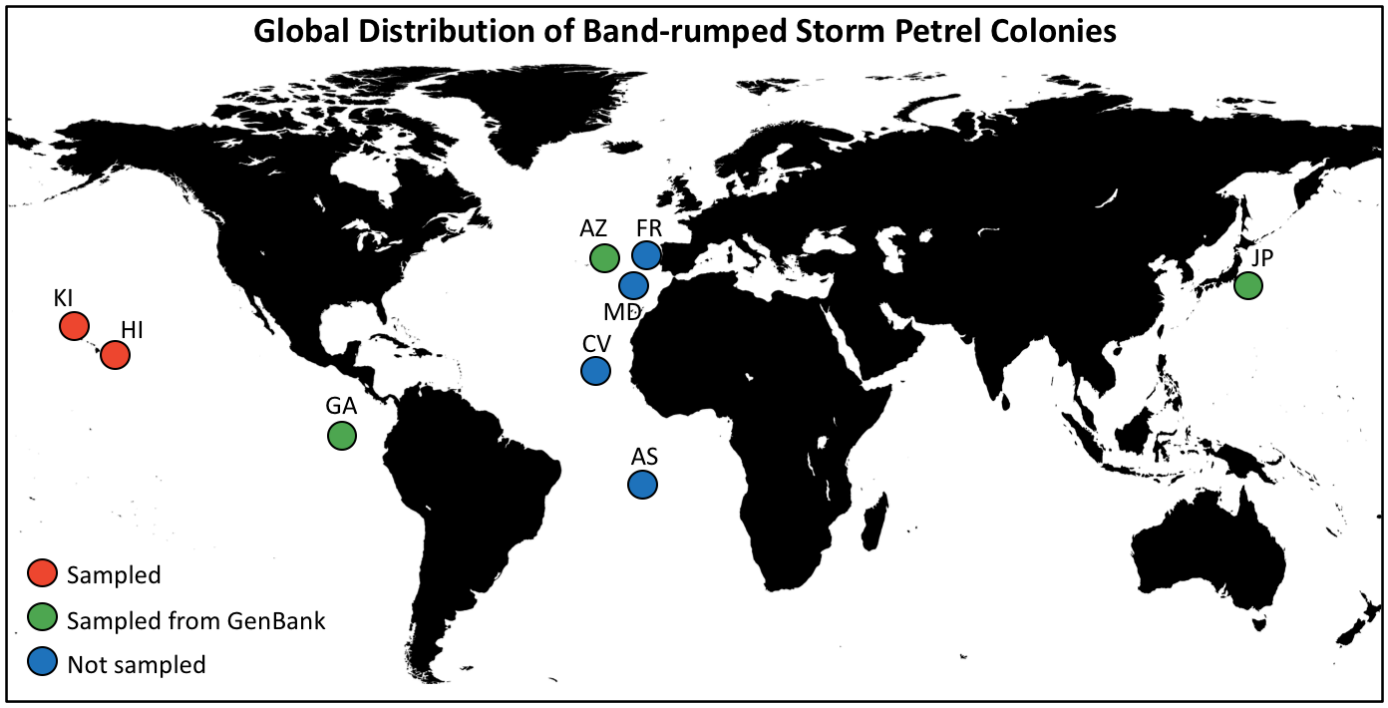

Figure 2.2 Global distribution of Band-rumped Storm Petrel (*Oceanodroma castro*) colonies (AS – Ascension, AZ – Azores, CV – Cape Verde, FR – Farilhoes, GA – Galapagos, HI – Hawai‘i Island, JP – Japan, KI – Kaua‘i Island, MD – Madeira)

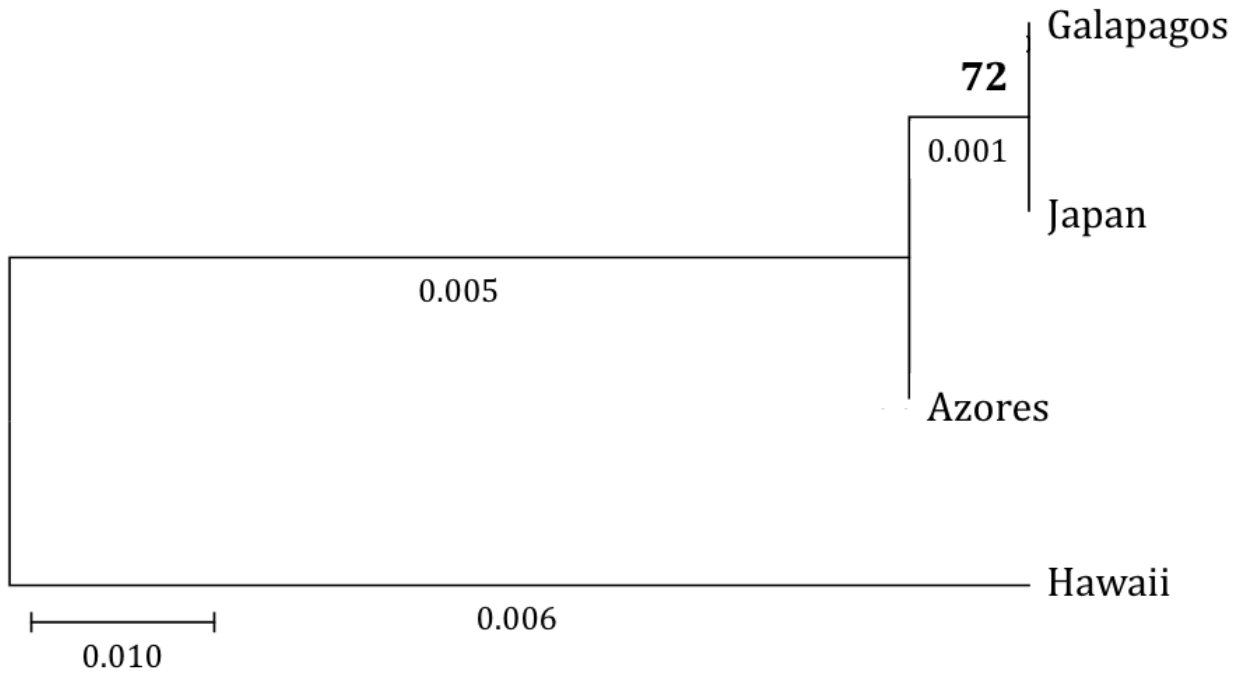

Figure 2.3 Phylogenetic tree of global populations of *Oceanodroma castro* (nuclear and mitochondrial markers) bootstrap Neighbor-Joining Tajima-Nei model constructed using MEGA7. The bootstrap value of 72, indicates the percentage of replicate trees which the associated taxa clustered together in the bootstrap test (1000 replicates). The other values are the branch lengths in the same units as those of the evolutionary distances to infer the phylogenetic tree (number of base substitutions per site).

Summary

This thesis represents a comprehensive examination of behavioral philopatry and patterns of population genetics across seabird taxa. Our research goal was to further understand behavioral and genetic philopatry within seabirds to inform conservation efforts. While some of the hypotheses presented in this research were supported, others contradicted our predictions.

Seabirds provide an interesting challenge when studying population dynamics: many are highly philopatric but also highly migratory, which influence dispersal and gene flow in opposing directions. Within the exploration of behavioral philopatry through use of long-term banding studies, we found dispersal to be less correlated to colony size and population structure and instead linked to with foraging strategy, taxonomic order, and geographic region. Across seabird orders, Procellariiformes, a historically philopatric order, showed no difference in genetic diversity to those in the Charadriiformes, a less philopatric order. The Band-rumped Storm Petrel, an endangered and philopatric seabird, had higher genetic diversity and population structure than hypothesized in the Hawaiian Islands. Population genetics of the endangered *O. castro* suggested moderate gene flow possibly due past population size, high mutation rates, and complex population structure. Although BSTP populations in the Hawaiian Islands had relatively high genetic diversity, there are still a multitude of threats to BSTP, from introduced predators to climate change. This study suggests BSTP in the Hawaiian Islands do not appear to be in danger of a genetics induced vortex but remain vulnerable to other threats (Gilpin & Soulé, 1986). Consequently, management efforts should continue conservation actions at existing colonies and seek to expand potential predator-free refuges, like Lehua Islet (Raine et al., 2017), to increase population size within the Hawaiian Islands.

Appendix 1: Microsatellite markers (*N*=153) identified by PANDASeq using next-generation ezRAD reads from *Oceanodroma castro*

Id	Forward Primer	Reverse Primer	Motifs (bases)
1	TGCCTCAGCTGTTTGTTTCC	GCAGCATGGAGGGAGATACC	TC(12)
2	ACCAGGAAAATACCGAGGTCC	ACACCCGTTATTGCTCAAAGG	TC(12)
3	GATCCCTGCATAGAGCCTGC	CCTGTAAACTGTCCCCTGGC	TC(32)
4	CTCATCGTTTGATGAACCCG	AATTCATCCCATGTTTCACGC	TC(14)
5	GATCTGAGGGGTTAGTGGCG	ACGTGAACATGAATGACGGG	AC(18)
6	CTTTCCATCCTCGCAATCG	GAGGAAACGTGGAAAGGTGG	TC(22)
7	ACAGCCTGTCCTGAGGATGC	GATCATCCCTTTGTCCTGGG	AC(12)
8	TGTTCAGTTTATTGGCTTTTGCC	GGCTGGATTTGAAGTGTGGG	AC(12)
9	CTTCACTTAAGGCCCATGCC	GGTGGTACCAGTAGTGGTTTAGTGG	AT(12)
10	CAACACGCACTTGAGACAGC	CAGATGTAGCTGACGTACGGG	AC(20)
11	GATCCACCAAGAACCACACG	TGCTACCCTGTTTCAGCAGC	AT(14)
12	TCGACGATTTGTGTGTGTGC	AATATCAATCTGCCGAGCCC	AC(14)
13	ATGCCATTATCTTCACCGGG	AAAACTGACTCCGCATTTTGC	TC(12)
14	TAAGATGCTGGTCGGTCGG	AAATCAACATGTGGCCTCCC	AC(26)
15	ATGGCCTTGCCAGAGATACC	CTATAAGACAGCACCCGCCC	AC(12)
16	AGTCATGAAAAGGAAGGCCC	GCACAAGGAAAGAAAGTGTAGTAGG	TC(16)
17	GACCCACGCAGTCAAATCC	CAGAGTCTGCTTAGGATTCTCCC	TC(14)
18	AACATTTACACATCGAGTAAGCAGC	ACACTTCCAGAGGGGACCG	AT(14)
19	ATGCAGTACGGTGGCAAGG	ATATGGCAGTCACGGTCACG	AC(14)
20	TCACGTTTGGAGGAAAAGGG	GATCCATGCTTGCTCCAGG	AC(12)
21	GGCAATCCAACTCCAACTCC	ACCTGAAGAAAACGCTTGGG	TC(12)
22	CAAAGCCTGTGTTGCTGAGG	CTCCTATGTGTTGGGTCCGC	AC(12)
23	CCTAAGGGTAGGGATGTGGG	GAAGACACTGGAGCTGTTGACC	AC(14)
24	AGTGAGTGACAGCCTGGACG	GTCTTCGGCGATACGAGCC	AC(14)
25	GATGGTGGTGGATATGGACG	ACATTCCGGAGTTGGTTTCC	AT(12)
26	CAAACACTTCCCACCCAACC	TGTGTGCATTTGTTTCTGCG	AC(12)
27	CCAATGATAGACTAGACCGGCG	TGAGGGTCTCACATGTTCGC	AT(12)
28	TTGTTGGACACTGTCGAGGC	TCAACACTGCCGTCTTCTCG	TC(12)
29	GTGTGTTGCTGTGTTGCACG	CAGCTTGATGGACGTTCTGC	AC(14)
30	GGTCTGAACTCTCAAAATATACAGGC	TGGTGCATAAGTGTTCTCAATGG	AT(12)

31	TGTACAGTTCGTTCGTCCCC	TGACTGCAGCAATCTTTGCC	AC(12)
32	CTGGCAGGGAGAATTATGGG	CGGGTGAGCTGAGATTAGGG	TC(12)
33	TGTACTAGCCATTGCCTGCC	ACTTTGCCTGCTGCATTTCC	AC(12)
34	GGTGCCTATAGTTGGCAGGC	CACATTGCCTTTACAGTTACTGCC	AC(14)
35	TGTGTCGGGTCTTGTATGGG	TCTGTCTCTTTGCAGACGGG	TC(14)
36	CGAGTCTCACATTGGGCTCC	CGTCCAGAGTTGTCCCTTCC	TC(24)
37	CTACAGCCAATGGCAACACC	CCTCGGAAGGAATCACTGACC	AT(20)
38	GCAGAAACGAGAATGATGGG	TCCAACTGGCAGTCAGAACG	AC(12)
39	TTAACATAAAACCTCCCACCCC	TCTCTCTCTGCTGTGCCTGC	AC(12)
40	CCTTTGGCACAGAATGAAAGG	GAGACCAAAATAGACAGGAGAAGAGC	TC(28)
41	ACTGCAGCAGACACACAGGC	ATAGGATGTGTGGGCAAGGG	AC(12)
42	GGTCGAGGATATGCCTTCCC	TCACAGGAGAAGTCAAAGGGC	TC(12)
43	TTTACCGATTCCGATGTGGC	CTCATGGATAAAGGACCGGG	AC(16)
44	CACAATTTATCTTGCCCGCC	GAGATAGTCAAAGAGAGCCCTGC	AC(12)
45	CGGGGAACTAGTCATCGAGC	CGACGTTGTTCGAGCAGG	TC(20)
46	GGGTAGATCGAGCAAATCCG	CAAAGGATTGATTCCCTCCG	AC(12)
47	ACCGCCCTTCTTCTACCTCC	GTTGGTCGTCGTACTGGTCG	AC(16)
48	TGCTTGCCAGTTCAATTTCG	GGACTTTCCAGAAGTCGGGC	TC(12)
49	ATGACACAGACTCGATGGGC	AAATACGTCGGACAGTCGGG	TC(14)
50	GCATGGCCTTTTCACTGTCC	GTCTTCAAGGAGCCACTGGG	TC(20)
51	TGCCACCAAGACTTCTTCCC	GCTAGATGTCGTGCTCGTGG	TC(14)
52	ATGTTTGAGCCCCATGTTGG	CTCCCTTGCTGTGTCATTGC	AC(30)
53	AGCTCTGATCTGCCCCTCC	AGCCTGCTTCTCTCTTTGCC	TC(14)
54	CACCATGTCACCACCAAAGC	ATGCCAACTCCTTGACCTCC	TC(12)
55	CCAGTCCTGTGACCATCAGC	CAGATGGACCAAACAGCAGC	TC(14)
56	CAAATCCCTGCAATTTTCGG	AAGAACTCACTTGGTGGCCC	AC(12)
57	CAGTCGTGTAGCTTGCAGCC	TTTGTTGGAGGTTGCTGTGG	AC(12)
58	TTTTGGGGCAATTTCTATGG	CTAATCCCTCCAAACCCTGG	AC(12)
59	AATCCCAGTTGCAGACACCC	AATGAAATGGCACAGCATGG	TC(24)
60	GCTCACCGGGAACTATTTGG	TAGCAAGTGCTCGTTCTCCG	TC(12)
61	TCCTAAGGAATCTCGAGGCG	CTTCCCCTTCTTCCATCCC	TC(18)
62	CTCTGCGGAGTTGTGACTCG	ACAAACCGACATACCCTGGC	AC(14)
63	AGCCGAAGCCACAGTCTACC	ATTCGGTATAGCGACCGGG	AC(12)
64	GAAAAGCTGCTCAACGCTCC	TTCACCTCTGAGAGCATCCG	AT(12)
65	GATCATGTGGTGAGATAAGCG	ATGTGTGAGGGAACAGGAGC	AC(12)
66	CTTCTGATTGTCACGAGCGG	GCGAAACGGTTCTTCAAAGG	TC(14)
67	GGAGACAGGAATGGGTGATGG	GCTATAGGCTGTCTGTCAGTGGC	AC(26)
68	CTCTCCCATCTTCTCCCAGG	GTCCAAGGGGAGAAGGAACC	TC(12)

69	GCAGCCAAGAAGACACATGG	GGGCCTAGTTTGGTGAGAGC	AC(16)
70	GGAGGTCTGGGTTTCTGAGC	GGCGTAGGACATCAGTTCCC	AT(18)
71	CCGTATCCAAAACAAAACGC	GATCGAAAAGGTTGCTTAACG	TC(18)
72	TTGCAAATTGCCCTTTATGG	TTGGGCTTAACTGGTGATTGG	AT(14)
73	GAAGAATTTCCCAGCAATCCC	TTAGGTGGTCGAGTGGAGGG	AT(18)
74	CAACAGAAGCAGCTTGGACC	GAAAACGTTGTGCCCAATCC	AC(26)
75	ATCCTGAAGACCCAGGATCG	AAATTCTTTTAAGCACTGGGAAGC	TC(18)
76	CCCAGAGCTGAAGGGAAGG	CATTCTTCCTGCCAACACCC	AC(22)
77	CACAACCGTGACATCGAACC	GAATACGAATCCTCCAACAGCC	TC(14)
78	TAGGTGCTCTGGCATTCTGC	AAGTCCAAAGCAGCCCTCC	AT(12)
79	AACCTCAGCTTCCTGCTTGC	AAGTTGATTGCACGTCCTCG	AC(12)
80	CTTCCTTGTTCCACTTCGCC	GCGTCCTTGTTAATGTGCGG	AC(12)
81	ATACCCCACACTCCGTCTCG	CTTTTGTCCTGCAAACACCC	TC(14)
82	GTACAAAGTGCCGTGCAAGC	CAGGAGACTTGGTGCATTGG	AC(14)
83	ACACGCAACGTACCACAAGG	GACTCGCTTCTCACCGTTCC	AC(12)
84	CACAGGTGAATTCAAGGGGC	AGCTCGTCAACCTTCATGGG	CG(12)
85	CACAAGACCATCGGATAGCG	TTACAGCAAATTCGGCAAGC	TC(22)
86	GGGTCTCTACAGTGCAGGGG	GAAGACGGCAGCAAAGAACC	AC(12)
87	TAGGAATGTGGCGATGATGG	ATCTCTCCGTGAGTGCCAGC	AC(16)
88	TAAACCCCACCTTCTGCTGG	CTGCTGGAGAGGCTTTGAGG	AC(12)
89	AGACCGTCAATGGGTCAAGG	GAAGACGACAGTGAAAGGCG	TC(14)
90	TGCACTAGAGCACACGTCCC	AGCCTCTCTCACAAGCCAGC	AC(12)
91	GGCATACTCTGCAGCTCACG	ATTCCGACACTCCTTGTTGC	AC(12)
92	GACTCCATCAGCACCAAGAGC	TCAGGCATTAAACAGCCTCG	TC(18)
93	ACTCCAACACACCCTCTCCC	TCAGCAGAGACAAGGCTTCG	CG(16)
94	ATCCAGAGAGCAAGCAAGCC	TGTTTGTGTTTCGGTCTGGC	AC(16)
95	CTTGCTTTTCTTCTCCTCTCCC	AATGGCTCAGGTTCTGCTGG	TC(14)
96	GCCCATGTACATACCAGAAAGG	ACTCGCCAAAATGAATCACG	AC(14)
97	AGAGAGGGGCTGAGCAGAGG	GACAGATCCCTTGGTCCTGC	AC(22)
98	GAAGCAATTTCAGGGCATGG	CACAGGTCGTTCGAGTGCC	AC(12)
99	TGAGCCCATTCAGAAGAAATCC	AAGCTGGCTGCTCAAGTTACG	TC(12)
100	TCATGCAAAAGAGGAGCTGG	CATTGATGGCGACTTTCAGC	AC(12)
101	ACAAGCCACCCGTAGTCTCG	AACCACGCCAAAAGACAAGG	TC(14)
102	AGCTCGGCATTTTCATTTGC	CGTATGGGCTGTGAGAGACG	AC(12)
103	AGACGAGATGAAAGCGGAGG	CGGTGTCCTCAAGACCTTCC	TC(12)
104	TCGGGTAAGTATCATCCGGC	TCCAAAGATGATGACTGGCG	TC(12)
105	CCAAGAAGAACAAGACCGCC	TGGTCAACACAGCACCAGC	AC(12)
106	TGCCAGAGATTACATACATGCC	AGCTGCTCTGATACCTGGGG	AT(14)

107	CATCGCATGATGTTTTCACG	AGAGGTTTAAATATTACTCCTCCGC	AT(12)
108	AAACCGGGTGTTGGGAGG	GACAAGGATGAGCGACCAGC	TC(12)
109	AAATACTCCCCACACACCCC	TCATACTTGTTTCTTTATTCCTGTTGC	TC(12)
110	GCTTCTGGGAAGAAAGCTCC	CTTGAGATCAGCCTAGGGGC	AT(12)
111	TTGTACGATGGCCTCTCTCG	AGAGGGATGAAACAGAGCCG	TC(16)
112	AGACAAGCCATTGTTTGGGG	CTGCTTTTCCCACCATAGCC	AT(12)
113	CTCATGCATTGAACAAGCCC	ACGGAACCAACAGATGGACG	TC(14)
114	GATCCAGTCCTGCATAGGGC	CTTCCATTGGGCATGTCTGG	TC(12)
115	GACGCGTTAGCTGGAGAAGG	ATCCCCACGGACAGGAGG	TC(24)
116	CGTGAACATCACCACCAACC	TTTGTTCCAGCAGCTTCACG	AC(12)
117	AAAGTTCATTCATGACGGCG	GGAGAAAGTGAGCAGTGGGG	TC(12)
118	TTTGTCTGTGATTACTGCTGCG	TTTTCGAATGAAAGTCGACCC	AT(12)
119	AAAATCCAATCCCCTGTCCC	AGCACTTCTCCATTGCTCCC	AC(14)
120	CTGGAACTCTGACGCGACC	ATCTGGATGCTTTTCCGTGG	TC(18)
121	GTTGGATTGCATTTGTTCGC	AAGTAGCGATTGTCCCGAGC	TC(12)
122	GATCCAGTCCTGCATTGGG	TTGAAAGAGACAGGATTTGAGTGC	TC(14)
123	CTTCTCTCGCTGCGTCTTGG	CTCGTCGTACTTGGCACTGG	CG(12)
124	GCATCTGCGAAATGAACAGC	TATCAAGAGCGGTGTGACGG	AT(16)
125	TCAGCTGCTGTCTCTTTGCC	CACACAAAGGAACTTTATTTAGTTTTGC	AT(16)
126	CCTGAGATCATGACCTGGACC	TGCTAATTTTGTGTCCTCTGTGG	TC(18)
127	CAACATCCCCAGATCTCTCTCC	TGGTGAAGATGTGCAAAGACG	AC(26)
128	GGCTGTTAGAGATGAGCCACG	TAAAGAAGGGACTGCCACGC	TC(12)
129	TTTGAGGAGCGAGAAATGGC	CGAACTGCAATGACTCCAGG	AT(18)
130	GGTTCCCTTTACCCCTCACC	CGGACTGGAAAGTTGAACTGC	AT(16)
131	GATCTGTCATCGGTGGATGG	CAGACTGGATTCGCTCATGC	AC(12)
132	GATTAAGTACTGCCTGTGTCTCTGC	GATCAGCTGGGAGCCTGC	TC(32)
133	AACATCAACAACCCAGGAACG	TTGTCACCCACGACTCTTCG	AC(26)
134	ACAGACGAGGACGACACAGG	GAGTTCATCGCAAGCTACGC	TC(12)
135	TCCACAATTCGCCAGTTCG	TGCTTACGCTTGGTCTTTGC	CG(12)
136	TCATGTCCGAACAGCATCG	ACCTGTTCATCCTGGGTTGG	AC(12)
137	ATGGTGGCATAGACAAAGCG	ATGGCTACATCACTGGTGCG	TC(18)
138	GCTTAGCCGGACAGTTTTGG	TCCGGTTCTTACAATTGGGC	TC(12)
139	CGTAGGATGGAGAGAAGGCG	GGACGAGTTTTGTCACCTCG	TC(16)
140	TGTATCTCGGCGATTTGTCG	CGATGAATAGAGCCATGTAGAATGC	AC(34)
141	TCGTCATGTCTGTCAGCCG	TGTAGTCGTTGATGTCGGTGC	AC(12)

142	ACGGTTTGTAAGTGCGGAGC	CAGAGACGACCCATCTGTGG	TC(12)
143	CACCGAGACTCTGAACTGAGC	TGCAGCAAGAGAAATCTTCACC	AC(12)
144	ATTCCTGCCACATGAAAGCC	GTGTGAGGTCTGGACTCCCC	AC(14)
145	GACGATGGCGATGTATCTGG	GGTGTTTTGGGCTTGCTAGG	TC(12)
146	CTCGAGTCCAATCTCCTGCC	GAGAGAAATGGTGGAGAAAAGAC C	AC(12)
147	TATTCAGGTCCGACACACGC	TGCGAATTGCTATGACAGGG	TC(24)
148	AAGAAAAGCCCCTACCACGC	GAGCCGAGCTCTTTGTACCG	AC(28)
149	TTGCAGTGAGCACTGTTTGC	GAGAGCGGTCTACGCATGG	TC(20)
150	CATATGCGACATAGGAGGAGC	TGTGTTTGTGTGCAAATACTACG	AC(12)
151	TGAAGAGACTAGATATGCAAGG GC	GGCACTAAGAAAGCAGTAGGGG	AC(12)
152	GAACCCAAGGCTCAGAGAGG	TGCAGGAGTCTGCTTCTCCC	TC(16)

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